A CONTRIBUTION TO THE BIOLOGY OF AMPHIPOREIA LAWRENCIANA IN NEWFOUNDLAND WATERS

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A CONTRIBUTION TO THE BIOLOGY OF *AMPHIPOREIA LAWRENCIANA* IN NEWFOUNDLAND WATERS

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ABSTRACT

In Newfoundland *Amphiporeia lawrenciana* is limited in its occurrence chiefly by the particle-size of the substrate and exposure of the beach. The species prefers substrate habitat in the particle size range of 125-2000 μ and it appears to recognize "home" substrate. At Salmon Cove 95% of the substrate is within the size range 125-1000 μ; at areas of greatest abundance of the animal in Newfoundland the same particle size predominates. A concentration of the species at Salmon Cove beach 25 meters from LWS during the summer months may shift seaward during the winter because of low water temperatures. A possible alternative explanation for the small numbers taken in winter samples might be that the animals burrow deeply enough into the sand to escape capture by the collection method used. Population numbers reach a peak at Salmon Cove in October when unsexable young constitute over 90% of the total; least numbers are present in January. Oogonia of the females enlarge in October and November; embryos are deposited in brood pouches in March and young are released in August. For a second brood embryos are deposited in June and released in the fall. The smaller male copulates at right angles to the body of the female and the latter assumes various reproductive hues during this season. Strong water currents created by pleopod beat aid the animal in swimming and burrowing. An efficient means of aeration of embryos in the brood pouches is provided by these water currents. The species is primarily an omnivorous filter-feeder preferring food within the particle-size range 125-250 μ but it will at times feed on large pieces of food.

At Salmon Cove it eats mostly plant food. Feeding rate may be reduced during reproductive periods for females.

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I INTRODUCTION

The sand-burrowing amphipod *Amphiporeia lawrenciana*, Shoemaker, 1929, belongs to the family Haustoriidae a group which inhabits quartz sands usually of low organic content (Sameoto 1969a). The family was originally named Pontoporeiidae by G. O. Sars in 1895; it was later called Haustoriidae by Stebbing in 1906 (Stephenson 1940). Bousfield (1962, 1965) enlarged it by including new species from the east coast of North America. Haustoriidae has two sub-families Haustoriinae and Pontoporeiinae; the species *Amphiporeia lawrenciana* belongs to the latter.

Species of this family have been found on both sides of the Atlantic; in the Pacific and in freshwater. On the western side of the Atlantic its range is north to the polar seas and southward to Florida (Dexter 1967). Sub-family Pontoporeiinae is found at high latitudes while sub-family Haustoriinae has radiated southward along Virginian and Carolinean shores (Croker 1967a). The two sub-families overlap in the Cape Cod region.

Within this family it is considered that the most efficient adaptation of body form for a sand-burrowing and a filter-feeding mode of life has taken place (Bousfield 1970). Bousfield states that it appears that the sub-family Haustoriinae is now in the process of replacing the more primitive Pontoporeiinae because of its more specialized and more highly adapted body form in the unstable beach environment.

The genus Amphiporeia contains three species: *Amphiporeia lawrenciana; Amphiporeia virginiana* and one undescribed, all endemic to temperate or cool-temperate American-Atlantic shores (Bousfield *op. cit.*). Specimens of the genus were first taken by Dr. Mary J. Rathbun at Grand Manan, Bay of Fundy (Shoemaker 1933). Bayne (1908) described but did not name the species *Amphiporeia lawrenciana* from collections made at Sept Isles, Quebec, in 1906. Although he described only one 8 mm. male animal, it is unmistakably *Amphiporeia lawrenciana*. It was from the collection made by net hauls from a depth of 40-45 m. in the Gulf of St. Lawrence by the Cheticamp Expedition in 1917 that Shoemaker named the animal in 1929.

Dexter (1967) states that *Amphiporeia virginiana* occurs on open sandy coastal beaches from eastern Nova Scotia to Myrtle Beach, South Carolina. *Amphiporeia lawrenciana* has a more northerly distribution in the western North Atlantic. Bousfield (1956) collected the species from Spindlers Cove, western Nova Scotia, and he states that it is among the haustoriid species believed to range southward at least into coastal waters of southern New England and probably throughout the Gulf of Maine (Bousfield 1965). Before this study it is likely that the most northerly record was Sept Isles, Quebec (Bayne 1908).

Twenty-nine beaches were sampled in Newfoundland during the summer of 1971; *A. lawrenciana* was found at eight of these beaches. On the west coast it occurred as far north as Shoal Cove on the Great Northern Peninsula, the most northerly known limits of its range, and on the east coast as far north as Sandy Cove, Fogo Island. Time did not permit a survey of beaches on the south coast but it is assumed

that the species could occur there in suitable habitat. Although the species is subtidal in its existence, it was collected within easy wading distance at low tide.

At Salmon Cove, Carbonear, the beach area chosen for intensive study of a population of *A. lawrenciana*, a total of 7694 animals was examined from thirteen monthly samples. Of these 4920 were unsexables (young without secondary sexual characteristics); 1923 were females and 851 were males. Sex ratio for the year was 7 females; 3 males although there were monthly variations during the reproductive season.

Mature males of the species are as a rule smaller than the females (Plate 1); their length range is 4-10 mm. with more than 46% at 6 mm. The female length range is 4-14 mm. with more than 27% at 9 mm.

Live animals appear light gray to the naked eye. Under a microscope, however, they show several distinct markings similar in both sexes. The ends of the coxal plates in the head region have white patches resembling careless brush strokes (Plate 2). White bands are located just anterior to the eyes and are also found on the peduncle and the first segment of antenna 1 and 2. Orange bands are found on the peduncle and the first segment of antenna 1 and 2 and also in patches in the posterior region.

The eye in the adult is black whereas in the embryo as early as stage C it is red (Plate 5). The eye color changes soon after hatching.

Except for taxonomic description and geographic distribution a search of the literature revealed that nothing else is known about the

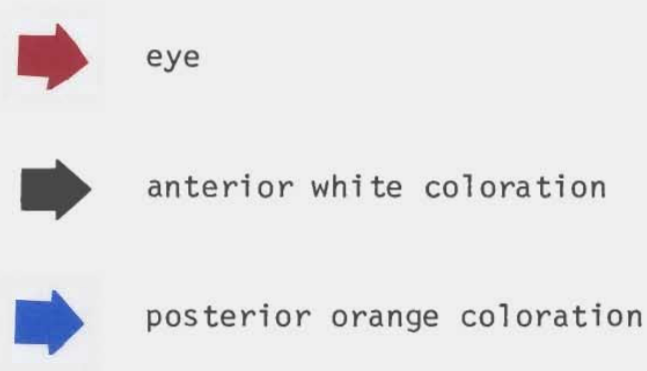
Plate 1.

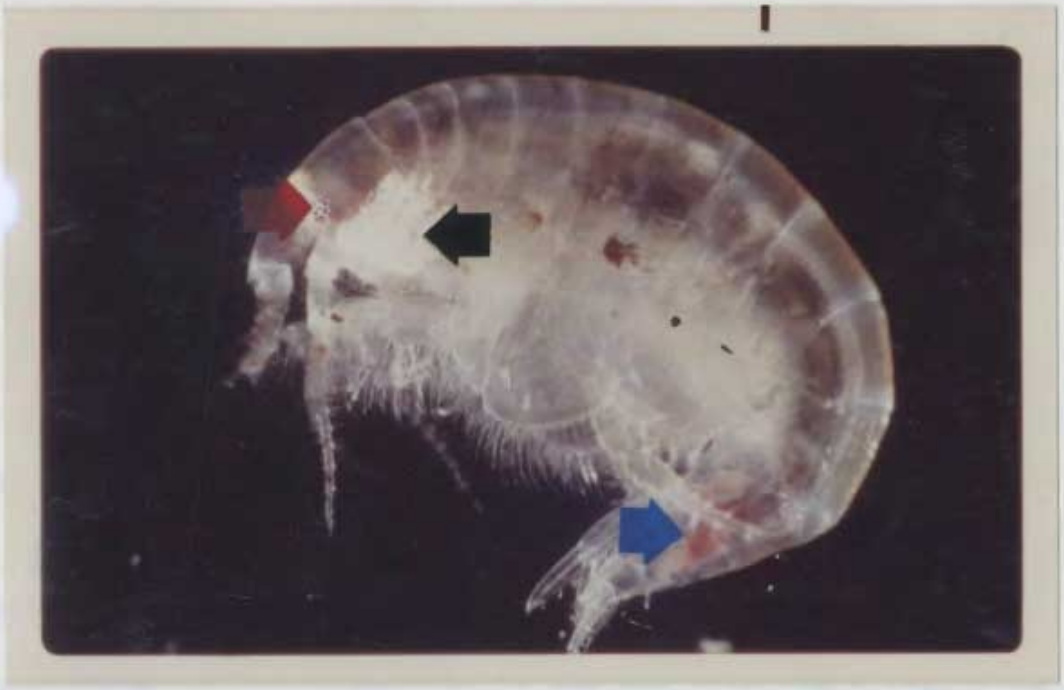
Amphiporeia lawrenciana showing the size difference between a mature male (top) and a mature female (bottom)


0 1 2 3
mm.

Plate 2.

Amphiporeia lawrenciana showing normal body coloration for the species. The animal shown is a female.





species *Amphiporeia lawrenciana*. The same holds for the genus Amphiporeia. It is hoped that this study will contribute some knowledge of the general biology of this animal.

The reproductive cycle and life history of *Amphiporeia lawrenciana* have been studied by taking thirteen sets of quantitative samples at five temporary stations established at Salmon Cove in October, 1970. Beach samples were taken generally at monthly intervals until October, 1971. Physical parameters have been recorded at Salmon Cove and throughout Newfoundland and an attempt has been made to determine some of the major physical factors influencing monthly abundance at Salmon Cove and distribution and abundance at beaches in Newfoundland.

Laboratory studies have been concerned with observations and experiments on swimming, burrowing and feeding habits as well as the species' ability to select particular habitat types according to the color and particle-size of the substrate.

The study is not exhaustive in any one area but a beginning has been made in several areas of the general biology of the species and of the genus.

II AREAS STUDIED

A. Salmon Cove

Salmon Cove, located on the western shore of Conception Bay (Fig. 1 and Plate 3), is an exposed sandy-beach area open to easterly and north-easterly winds off the Atlantic Ocean. During the fall, winter and spring sampling periods moderate to heavy surf action existed; even during the summer the water was rarely calm. Slushy ice filled the cove during January and February but at no time was it completely frozen over.

The estuary of Salmon Cove River is located west of the cove. It is separated from it by a prominent rock island a little offshore. The cove itself was selected as the study area (Fig. 2.)

Gray-black shale sand of relatively fine texture constitutes almost the entire beach. The bottom of Salmon Cove extending over 200 yards from LWS consists of similar material. At the extreme south end of the beach a small area consists of cobbles of varying sizes. Approximately 100 yards back from HWS shale cobble and boulders appear more frequently in the sand.

The sampling site extends 163 meters from the rock island on the north to a steep rock face at the south. A sand bar between the rock island and the main beach is exposed at low tide, but a narrow channel approximately three meters in width separates the end of the bar from the rock island so that some small amount of mixing may occur at high tide from freshwater out of the estuary. Coarser sand is found

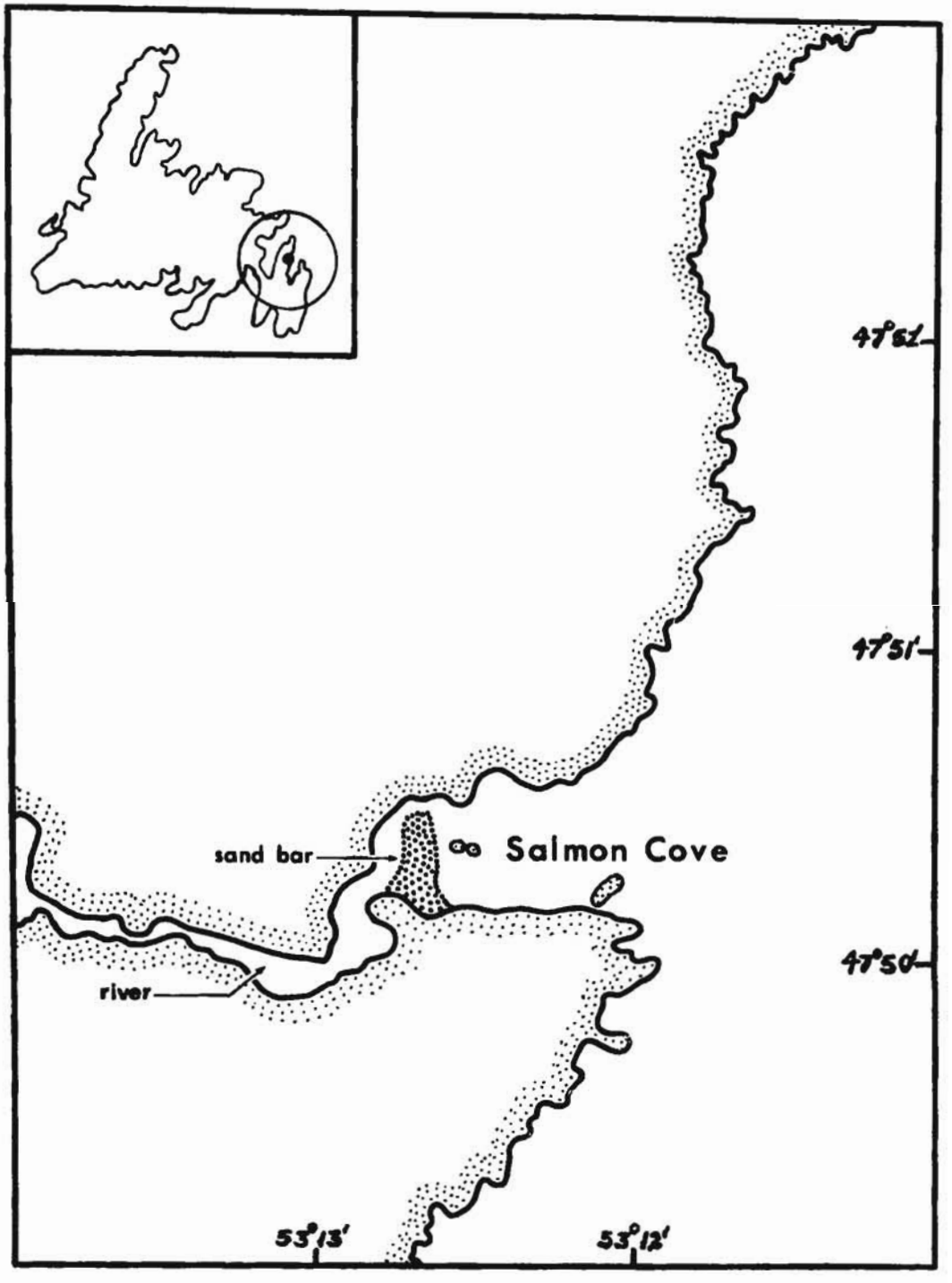


Fig. 1. Map of the western shore of Conception Bay showing the Salmon Cove sampling site.

Plate 3. The Salmon Cove site.

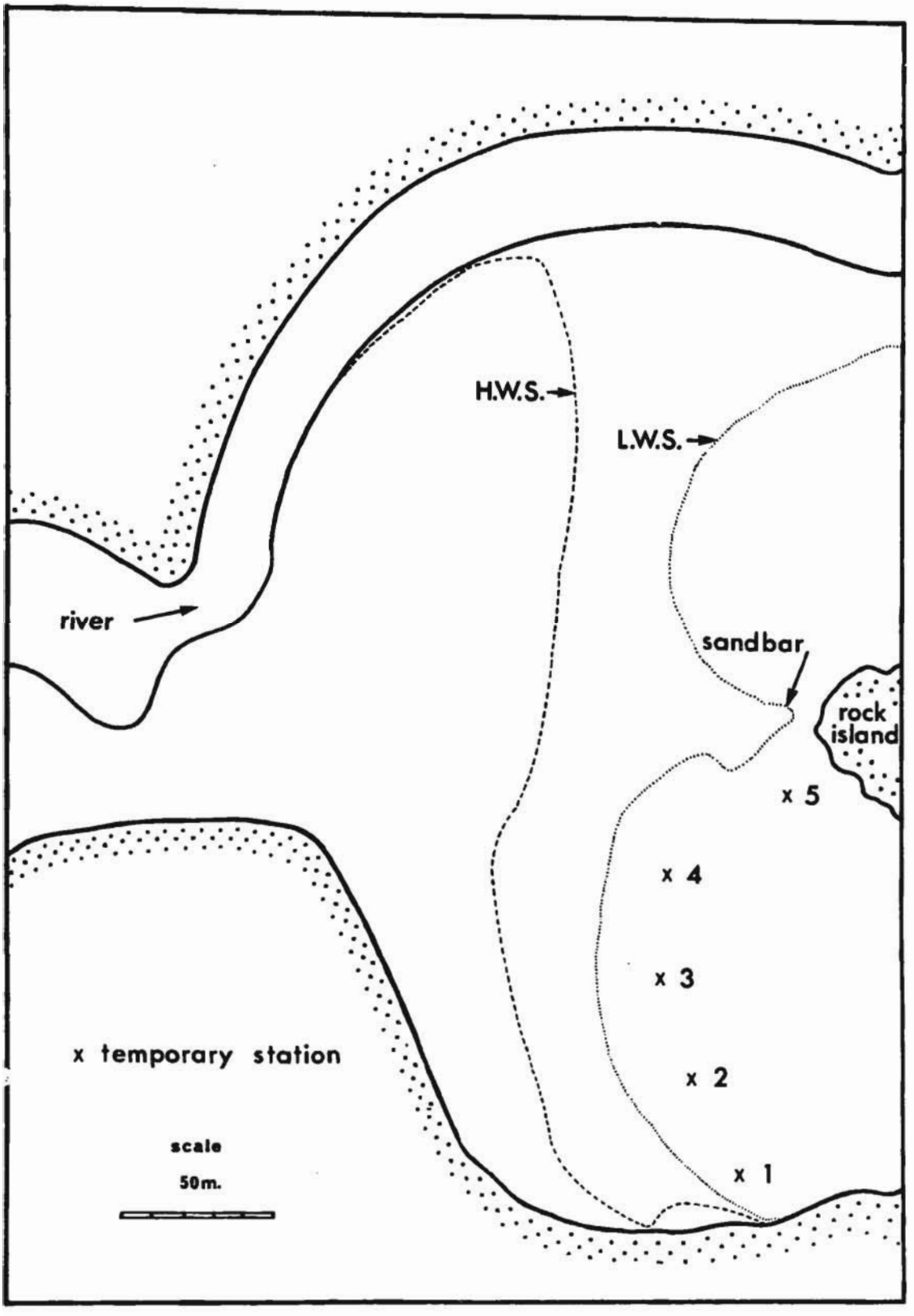


Fig. 2. The Salmon Cove sampling area.

in and near the channel.

The location of five stations established permitted comfortable wading during the fall and winter of 1970-71 (Fig. 2). Shifting contours of the bottom caused by heavy surf action during storms in March and April put stations No. 1 and 2 under more than a meter of water making sampling more difficult. Shifting sands in the surf zone often made the station locations almost unrecognizable from month to month.

The area has the usual fauna associated with sandy beach habitats. *Gammarus lawrencianus* and young *Nereis diversicolar* were taken with *Amphiporeia* samples particularly in the summer. These two species were taken pelagically in abundance in plankton tows at high tide during July. Broken fragments and whole empty tests of *Strongylocentrotus droebachiensis* were commonly mixed with the sand although the animal itself was not found inshore. *Mytilus edulis* were found attached to bedrock and algae surrounding the area but none were found living on the sand.

Shortly after the caplin (*Mallotus villosus*) had spawned and moved off from the shoreline in late June and in July, several large eelpouts (*Macrozoarces americanus?*) were observed in shallow water in pursuit of stray caplin. None of the eelpouts were captured and the stomachs of 10 caplin examined were empty.

Fucus vesiculosus and *Laminaria digitata* abound attached to the bedrock near the study area. After a storm many pieces of these algae were found scattered along the beach but within a few days the beach was clear again.

B. Other Areas

Fig. 3 gives the locations in Newfoundland of the 29 beaches sampled during the summer of 1971. They are located from Cape Freels on the north-east coast to Hampden in White Bay and on the west coast from Cape Ray northward to Pistolet Bay.

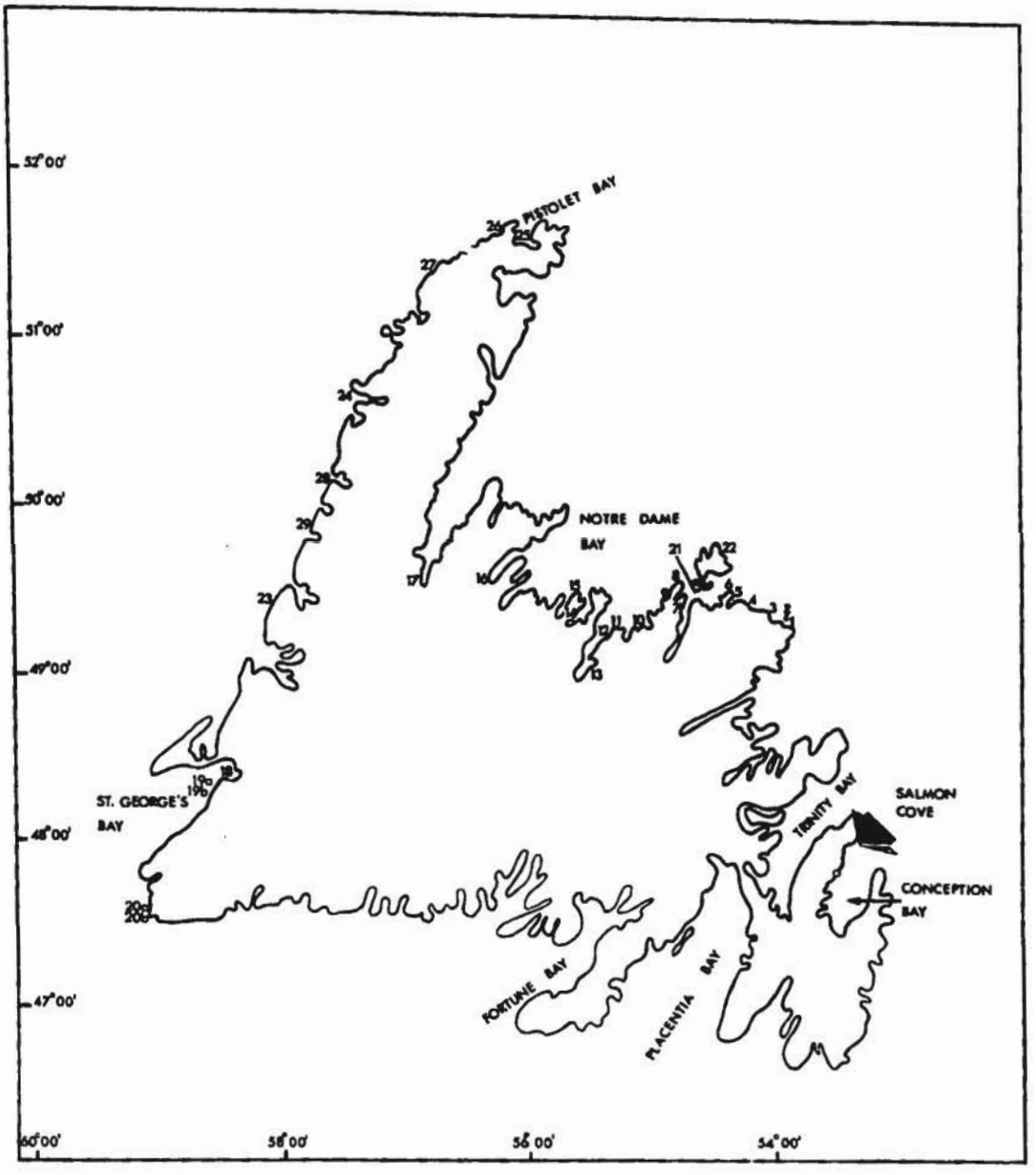
The beaches were selected to represent a variety of habitats within the sandy or cobble-beach environment. Deadman's Bay (Fig. 3, No. 3 and Plate 4a) and Embree beach (Fig. 3, No. 11 and Plate 4b), both located on the north-east coast, perhaps best represent the two extremes for those sampled.

Deadman's Bay beach (Plate 4a), extends more than half a mile. The entire beach has sand relatively fine in texture and it is well exposed to surf action. Seawater temperatures and salinities probably are very similar to those at Salmon Cove throughout the year since both are exposed to the open ocean. Embree beach (Plate 4b), on the other hand, has substrate ranging from coarse sand to large cobbles with the coarser substrate predominating. The cove is well protected receiving very little disturbance except when winds blow directly into it. The other beaches sampled show a range of characteristics between these two extremes.

Garbage dumps were frequently observed at the beaches visited, but the only obvious incidence of water pollution, apparently from domestic sewage, was found at Musgrave Harbour on the north-east coast (Fig. 3, No. 5).

Fig. 3. Map of Newfoundland showing locations of twenty-nine beaches sampled in 1971.

1	Windmill Bight	17	Hampden
2	Southern Brook	18	Black Beach-Stephenville X.
3	Deadman's Bay	19A	Flatbay (outside)
4	St. Shore Brook	19B	Flatbay (inside)
5	Musgrave Harbour	20A	Cape Ray (inside)
6	Ladle Cove	20B	Cape Ray (outside)
7	Victoria Cove	21	Indian Island
8	Summerford	22	Sandy Cove
9	Comfort Cove	23	Trout River
10	Michaels Harbour	24	Port Saunders
11	Embree	25	Pistolet Bay
12	Browns Arm	26	Boat Harbour
13	Sandy Point	27	Shoal Cove
14	West Arm-Pt. Lemington	28	Portland Creek
15	Leading Tickles	29	Belldowns Point
16	Goodyears Cove (North).		


52°00'
51°00'
50°00'
49°00'
48°00'
47°00'
60°00'
58°00'
56°00'
54°00'
PETOLET BAY
NOTRE DAME BAY
ST. GEORGE'S BAY
TRINITY BAY
SALMON COVE
CONCEPTION BAY
FORTUNE BAY
PLACENTIA BAY

a.

b.

Plate 4. Two beaches sampled in Newfoundland:
a) Deadman's Bay; b) Embree beach.

III METHODS AND MATERIALS

A. Measurements

1. Physical and Chemical Factors

Temperature measurements at Salmon Cove began in October, 1970; salinity and per cent organic content of the substrate measurements began in November, 1970; and suspended matter in the seawater measurements began in January, 1971. All samples for these parameters were collected at monthly intervals except in May when two collections were made. The results obtained from five substrate samples collected in June and July, 1971, were used for determination of particle-size composition. All sampling ceased in December, 1971.

These parameters (escept for organic content of the substrate) were measured at 29 other beaches in Newfoundland during the period June to August, 1971.

Temperature

Temperatures were measured with a mercury Centigrade thermometer (-10° -- +110°C) at 8 - 10 cm. below the surface for seawater and 2 - 4 cm. below the surface for substrate.

Salinity

One sample fo seawater was obtained at each of stations No. 2 and 4 and returned to the laboratory. Collection bottles were of 167 ml. capacity with lock-on stoppers. At the laboratory specific conductance

was obtained by a CDMC conductivity meter and converted to salinity (p.p.t.). The mean of the two samples was recorded.

Substrate Organic Content

The simple ignition method was used to determine the per cent organic content of the substrate after the manner of Dennell (1933) and Trask (1939). The sample was obtained at station No. 3 at Salmon Cove (Fig. 2).

Absolute values are not necessary since the objective was to obtain relative values. Aggregates of substrate were not considered to be a source of error (Enquest 1949) but the presence of carbonates could have affected the results (Beanland 1940). Carbonates in the substrate could vary (e.g. seasonally) although there were no obvious changes in the number of test and shell fragments present. If the variation were not great, these would have caused a small error for each sample and the ratios of monthly values would be similar to those obtained if carbonates had been considered.

Seawater Suspended Matter

A seawater sample was removed consistently from the same location each month at Salmon Cove and about mid-beach for the other areas. It was frozen if not analysed immediately.

From the sample a one liter volume was removed and filtered through a desiccated 0.8 μ Millipore filter in a suction apparatus. The filter and suspended matter on it were dried for 24 hours at 60°C and weighed to the nearest 0.1 mg. Original weight of the dry filter

subtracted from the weight of the dry filter plus the suspended matter on it gave the weight of suspended matter in the seawater (milligrams/liter). The process was repeated for a second liter of the sample and the mean recorded.

In view of the unsettled arguments not only concerning the accepted filter size to separate dissolved from suspended material in seawater but, as well, the importance of dissolved material as food for organisms (Krogh 1931; Armstrong and Atkins 1950), it was thought quite justifiable to arbitrarily select a 0.8 μ filter to separate the suspended material in seawater and to assume that most of this material is organic. Again, since relative monthly values only are considered important at Salmon Cove and to compare areas in Newfoundland, the results are considered reasonable for the study.

Substrate Particle Size Composition in Per Cent

Five samples of substrate from Salmon Cove were analyzed for particle size composition and the mean for the beach was recorded. The first two in June came from stations No. 1 and 5 (Fig. 2). The three in July came from stations No. 1, 3 and 5 (Fig. 2).

Each sample was placed in a beaker and covered with .01 N $Na_2C_2O_4$ to disaggregate the particles. The mixture was poured through a 63 μ sieve and the filtrate was saved. This was again filtered; dried on the filter paper at 105°C and weighed. Weight of the dry filter paper subtracted from this result gave the weight of substrate < 63 μ in size to the nearest .01 mg.

Residue left on the 63 μ sieve was dried at 105°C and sieved

through a series of graded sieves (Table 1). Eight particle-size ranges were obtained by these means. Weight was obtained and per cent was calculated.

Since in this technique the $Na_2C_2O_2$ was not washed out, a small error may have resulted for all weights.

Table 1

Sieve sizes and substrated particle-size ranges obtained in substrate composition analysis

Sieve Size, μ	Substrate Particle Size, μ
63	< 63
125	63 - 125
250	125 - 250
500	250 - 500
1000	500 - 1000
2000	1000 - 2000
4000	2000 - 4000
	> 4000

2. Biological Factors

Size of Oogonia

Table 2 gives the oogonia size classes used. These are arbitrary divisions which were set up after a number of preliminary measurements had been made from females collected throughout the year. They are similar to the divisions made by Steele and Steele (1970a and b) for *Gammarus setosus* Dementieva and *Gammarus obtusatus* Dahl.

Table 2

A. lawrenciana: size classes of oogonia and oocytes*

Class	Mean size range, mm.	Description
1 (Oogonia)	< 0.15	No apparent differences apart from that of size were observed for the classes.
2 (Oocytes)✓	0.16 - 0.24	
3 "	0.25 - 0.34	
4 "	0.35 - 0.45	
5 "	> 0.45	

* Preserved in 70% alcohol.

✓ All oocyte classes in ovaries called oogonia in text and graphs.

The procedure followed after the classes had been established was to measure three representative ova from each set of ovaries to the nearest 0.01 mm. using a micrometer eyepiece in a Bausch & Lomb dissecting microscope. Size for each was obtained using the formula:

$$\frac{\text{length} + \text{width}}{2}$$

Mean size of the representative ova was used as the size of all the ova in the ovary of each female. The number of ova in this class was counted and tabulated.

Class 1 oogonia were generally found in immature females or those without setae on the oostegites; class 5 were found in mature females with long setae about to deposite embryos into the brood pouch.

Embryo Size

Table 3 gives the embryonic stages established for the species *A. laurenciana* in this study. The number of animals used to obtain the size ranges are given in the table. These were selected from samples collected throughout the year although the majority came from collections made from mid-May to August when the greatest range of embryos in various stages of development was available in the samples. Representative C- and D- stage embryos and hatched young are shown in Plate 5.

These divisions are based more on sight characteristics than on actual size measurements. The classes are similar to those used by Steele and Steele (1969) for *Gammarus duebeni* Lillij. The size ranges were set up by first selecting three embryos from each animal. Size for each was obtained using the formula:

$$\frac{\text{length} + \text{width}}{2}$$

Mean size of the representative embryos, measured to the nearest .01 mm., was tabulated. This procedure was repeated for embryos of the same stage from each animal. From these measurements the range for each stage was established and the mean (weighted) for each stage calculated.

Mean sizes for both the oogonia and the embryos in live animals would probably be somewhat larger since all measurements were made on specimens preserved in 70% alcohol.

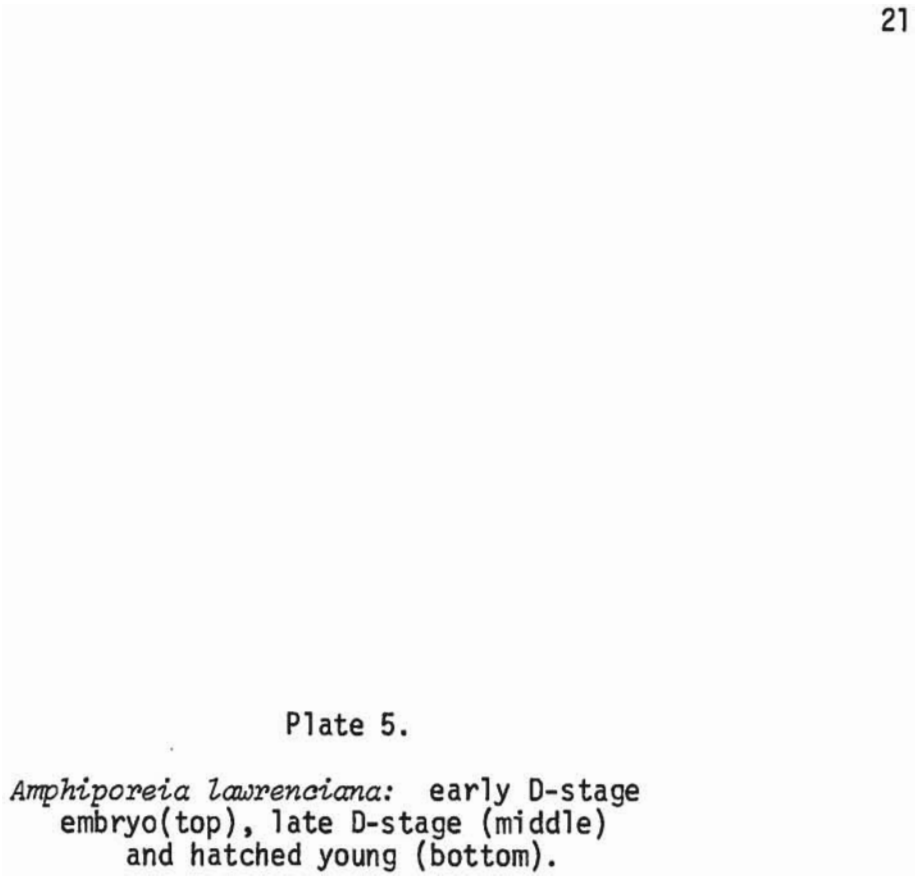


Plate 5.

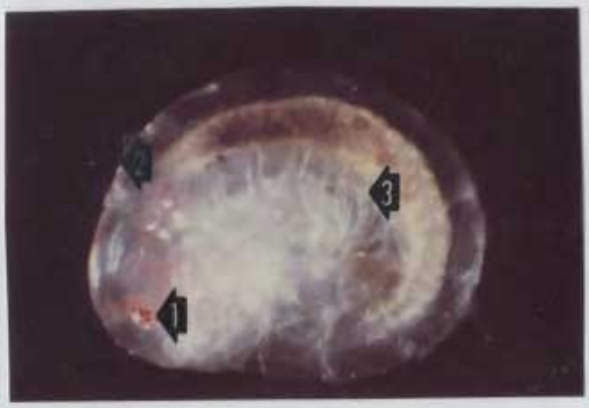
Amphiporeia lawrenciana: early D-stage embryo(top), late D-stage (middle) and hatched young (bottom).

1 eye

2 segmentation

3 appendage


1


2
3
1


2
1
3

Table 3

A. lawrenciana: Sizes and Stages of Embryos*

Stage	Number of embryos	Mean size, mm.	Range	S.E.	Description
A	16	0.829	0.70-0.95	0.018	Eggs clear; embryo indistinct.
B	19	0.853	0.70-1.00	0.022	Embryo indistinct; cells obvious; beginning of segmentation; cephalothorax separates from abdomen.
C	6	0.863	0.80-0.95	0.026	Embryo distinct; eyes developing.
D	18	0.913	0.75-1.05	0.020	Segmentation complete; eye and appendages developed.
Hatched	18	1.389	0.90-1.65	0.145	Membranes break and animal straightens

* Preserved in 70% alcohol.

Animal Length

Animals preserved in 70% alcohol were measured in seawater in a Petri dish to the nearest 1 mm. using a Bausch & Lomb dissecting microscope (10X) with a mm. scale underneath the Petri dish on the microscope stand. Measurements were made from the peduncle of antenna 1 to the end of the telson.

B. Sampling

For each station sampled at Salmon Cove a 0.1 M.^{2} grid was placed on the bottom and the substrate inside removed with a scoop to a depth of

12 - 15 cm. This material containing the animals *in situ* was placed in large plastic bags and returned to the laboratory for retrieval of the animals. Only one such sample was obtained at each of the beaches throughout Newfoundland, although a considerable amount of random sampling was done all over the beach at each site to ensure that the animals were not missed in the one quantitative sample.

Within 24 hours after returning from the field the amphipods were separated. Care was taken to keep the temperature low prior to sieving since it was found that the animals were much more easily seen and removed if alive.

Two sieves were used to separate the animals from the sand. It was found that the larger sieve (mesh diameter 0.4 cm.) removed all the large substrate particles as well as most of the larger animals. The smaller animals were observed with some difficulty when large substrate particles were present. These were removed with relative ease from the smaller substrate particles caught on the second sieve (mesh diameter 0.1 cm.). Fine sand grains passed through both sieves.

Specimens of *Amphiporeia* together with any captured associated macroorganisms in the sample were preserved in 70% alcohol. Numbers from the five stations were combined.

To determine the distribution of *Amphiporeia* with respect to depth of the water 0.1 $m.^2$ samples were collected by scuba divers in the manner described for field stations on only one occasion, July, 1971. A transect ran from HWS on the beach vertically from the shoreline for a distance of 100 meters to a water depth of approximately 1.5 meters at the outside end. Starting at the 25 meter point four samples were taken

at 25 meter intervals. The substrate with the animals *in situ* was removed and preserved at the laboratory as described.

A series of plankton tows was made on July 20-21, 1971, over a 24-hour period and all specimens of *Amphiporeia* and associated organisms removed and preserved in 70% alcohol. The plankton net was metal frame construction 732.6 cm.^{2} at the mouth with netting eight meshes per centimeter mounted on a metal frame sled which kept the bottom of the mouth eight centimeters off the bottom.

C. Laboratory Observations and Measurements

1. General Observations

General swimming, burrowing and reproductive activities were observed in holding tanks at the laboratory. Observations and measurements on burrowing depths were conducted using a small, plexiglass chamber (dimensions: 10 X 10 X 2.5 cm.) filled to a depth of 6 cm. with substrate. A mm. scale was attached to the outside of the chamber and read with the aid of a Zeiss dissecting microscope attached to a swivel stand as the animals burrowed close to the side. Much patience was required using this procedure since only about one out of 15 animals burrowed close enough to obtain a measurement. The distance of the distal end of the peduncle of antenna 1 was used as a reference point to measure the distance from the surface to the nearest 0.1 mm. Length of each animal was measured to the nearest 0.1 mm. in the way already described for field samples collected.

2. Swimming and Feeding Currents

Swimming and feeding currents were observed with the animals attached in seawater by the dorsal surface to the bottom of a Petri dish with petroleum jelly after the manner of Croker (1967a). It was found that normal swimming and feeding movements continued while the animals were in this position. A Bausch & Lomb dissecting microscope (10X) was employed for this purpose.

Water currents were easily observed by use of starch granules stained with iodine as first used by Cannon and Manton (1927) and later by Dennell (1933) both of whom found it very effective.

3. Gut Contents

To observe gut contents live animals recently brought from the field were pulled apart with forceps and the whole digestive tract removed intact. A semi-permanent slide was made when the gut was broken open on a clean glass slide and its contents covered with liquid glycerol jelly and a cover slip affixed.

The slides were later analysed under high power (1000 X), phase 3, of a Zeiss compound microscope. The following six food categories were established: detritus; amphipod integument and appendages; diatoms and unicellular, filamentous and multicellular algae.

4. Mouthpart Measurements

Maxilla 2 was removed from each specimen under a Bausch & Lomb dissecting microscope (10X) and a semi-permanent slide was prepared using turtox mounting medium as a combination mounting-staining medium.

Measurements were made under medium power (400X), phase 2, of a Zeiss compound miscroscope. Distances between the setae of each lobe were measured using a micrometer eyepiece in a manner shown in Fig. 4. to the nearest 1 μ. Length of each animal was found to the nearest 0.1 mm. in the way already described for field samples.

5. Length-Weight Measurements

Length of each animal was measured to the nearest 1 mm. as described.

Weight was obtained by removing the animals from 70% alcohol where they had been preserved for approximately two weeks; blotting on paper towel until no alcohol spots appeared and placing them on the stand of a Satorius balance (200 g. capacity). Measurements were made to the nearest 0.1 mg. Three animals were measured for each 1 mm. length class for animals of length 5-14 mm. for females and 5-9 mm. for males and the results averaged.

D. Feeding Experiments

1. Particle-Size Selection

Plate 6 shows the experimental setup for the feeding experiments. *A. lawrenciana* were offered each food choice in plastic containers 13 cm. long; 13 cm. wide and 6 cm. high filled to a depth of 3 cm. with substrate from Salmon Cove. Water entered via a small hole in the top through which a length of glass pipe was inserted. This was attached to rubber tubing 7 mm. in diameter connected to a glass water reservoir. Three

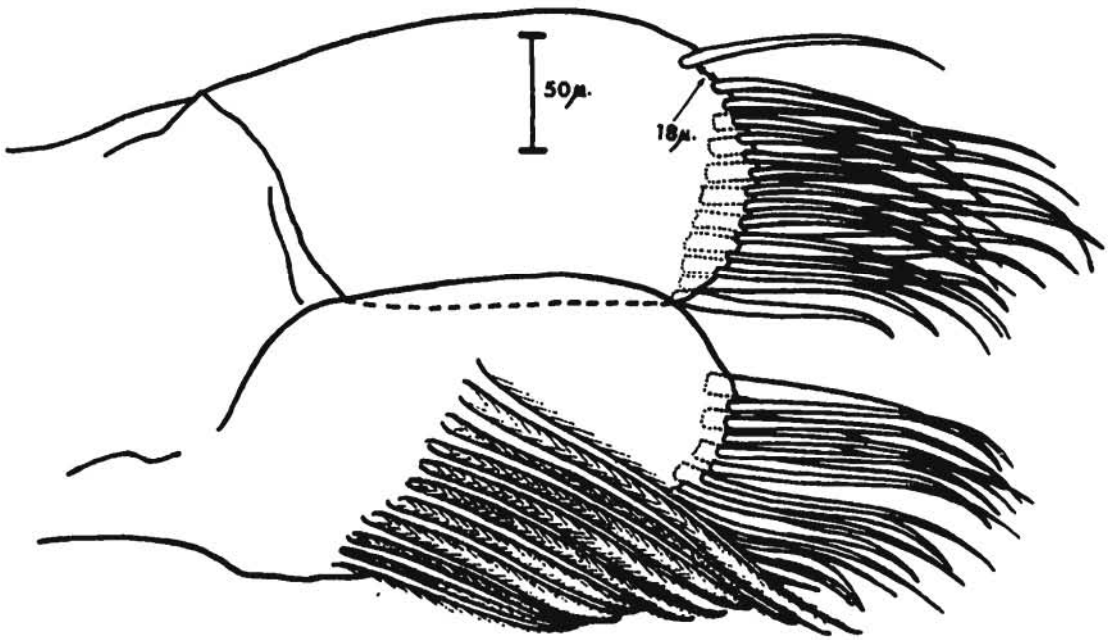


Fig. 4. Maxilla 2 of *Amphiporeia lawrenciana* showing method of measuring between the setae.

Plate 6.

Experimental setup for the feeding experiments.

drains consisting of short lengths of plastic tubing 12 mm. in diameter were placed in the sides of each container. Cotton screen 8 meshes per centimeter covered all inlets and outlets.

Table 4 gives the food particle-size choices offered in the first experiment conducted March 19-20, 1971. *Fucus vesiculatus* was broken up in an electric food homogenizer and passed wet through a series of graded sieves to obtain the particle-size ranges. Each food size was then stained with non-toxic, brilliant cresyl blue stain and washed thoroughly to remove free stain.

Equal volumes of food of each particle-size range was placed with three animals in each container for 22 hours. Then, each animal was killed and the gut contents examined under a Bausch & Lomb dissecting microscope (10X) for stained food particles.

In the second experiment, conducted April 27-28, 1971, the particle size category of > 4000 μ (Table 4) was substituted with one of < 63 μ. Non-toxic, fast red stain was used and the number of animals per container was increased to five.

In the third experiment, conducted March 19-20, 1971, the particle size choices offered were the same as the second but the number of animals per container was reduced to five and brilliant cresyl blue stain was used again since it was found to be far more easily detected in gut contents than fast red.

Any differences in the numbers of animals per container originally used and the number per container appearing in the results is due to a small number of animals escaping from the containers in the course of the experiments.

Table 4

Food and Substrate sizes used in Feeding and substrate selection experiments

Container Number	Particle-Size Range, μ
1	63 - 125
2	125 - 250
3	250 - 500
4	500 - 1000
5	1000 - 2000
6	2000 - 4000
7	> 4000
A	(1/3)* 63- 125: (2/3) 125- 250
B	(2/3) 63- 125: (1/3) 125- 250
C	(1/3) 125- 250: (2/3) 250- 500
D	(1/3) 250- 500: (2/3) 500-1000
E	(1/3) 500-1000: (2/3) 1000-2000
F	(1/3) 1000-2000: (2/3) 2000-4000
X	Unsorted substrate from Salmon Cove

* Figures in brackets give the volumetric proportion of each size range (applicable to substrate experiments only).

A control for each experiment consisted of one container with animals which were fed no food except that coming through the running seawater system.

In the fourth experiment, designed to test any differences in particle-size of food ingested with animal size, 10 small (5 - 6.5 mm); 10 medium (7 - 8.5 mm.) and 10 large (9 - 10.5 mm.) animals were placed separately in three containers and offered only one food particle-size range (63 - 125 μ). Brilliant cresyl blue stain was again used; the time and method of analysis were the same as before. This experiment was conducted May 6-7, 1971.

Experiment 5 with control, conducted on May 9-10, 1971, was a duplicate of experiment 4.

In experiment 6, conducted on May 10-11, 1971, only females with and without embryos in the brood pouches were used. The purpose was to determine any differences in females capacity to feed in the ovigerous and non-ovigerous condition. All other aspects were the same as in experiments 4 and 5.

Experiment 7, conducted on July 13-14, 1971, was designed to show any differences in the feeding of males and four different types of females (Table 5). All other aspects of this experiment were the same as in experiments 4, 5, and 6, except that one particle-size range of food offered was 250-500 μ.

Table 5

Types of *A. lawrenciana* used in feeding experiments

Container number	No. animals container	Sex	Type	Length, mm.
1	5	male		5.0 - 6.5 (mean - 5.8)
2	5	female	With long setae, without embryos.	7.0 - 8.5 (mean - 7.2)
3	5	female	With A-stage embryos.	7.0 - 7.5 (mean - 7.3)
4	5	female	With D-stage embryos.	7.5 - 9.0 (mean - 8.1)
5	5	female	With hatched young.	7.5 - 9.0 (mean - 8.5)

2. Food-Type Selection

After several preliminary experiments only one experiment was conducted on food type selection on May 11-12, 1971 (Table 6). Each food was macerated and contained the particle-size range 63 - > 4000 μ and stained with brilliant cresyl blue.

Table 6

Types of food used in the food type selection experiment

Container number	Number animals container	Food type offered
1	9	*Macoma balthica* - with shell.
2	9	*Placopecten magellanicus* - without shell.
3	9	*Laminaria digitata.*
4	9	*S. droebachiensis* - with test.
5	9	*S. droebachiensis* - without test.

E. Substrate Selection Experiments

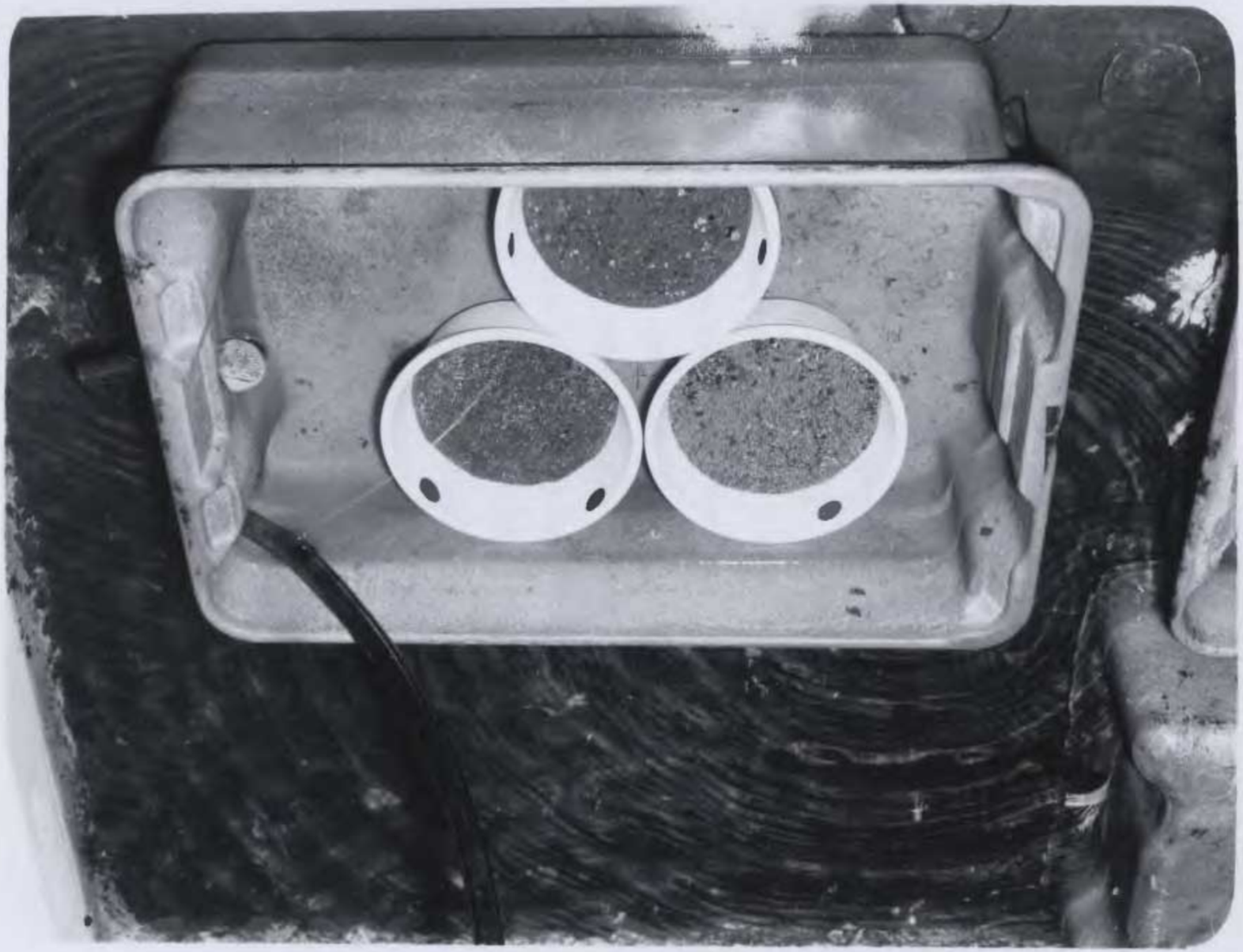
1. Color

Plate 7 shows the experimental setup for each of six substrate color selection experiments conducted on May 10-18, 1971. *A. lawrenciana* were offered a choice of green, black or red substrate in cylindrical plastic containers 14 cm. in diameter and 10.5 cm. high, filled to a depth of 6 cm., submerged in one holding tank and supplied with running seawater.

The green and black substrate came from Salmon Cove. The former contained a large amount of sea urchin (*Strongylocentrotus droebachiensis*) test and spine fragments which were primarily responsible for the green coloration. The latter was black shale sand. The third type of substrate taken from the bottom of Logy Bay probably derives its red coloration

Plate 7.

Experimental setup for color substrate selection experiments.



from iron oxide. Particle-size range was 500 - 1000 μ for all three substrate choices and *A. lawrenciana* had been found living in such material at both locations.

Sixty animals were used in the three and 90 in the three other experiments. At the beginning of each experiment the animals were removed from holding tanks and dropped onto the water surface above the color choices equi-distance from each. Each experiment ran for 22 hours when the substrate in each container was sieved and the animals removed and counted. Animals found outside the substrate containers (but inside the holding tank) were also counted in an attempt to determine the number rejecting all types of substrate offered.

Five control experiments were conducted in conjunction with both the substrate color selection and the substrate particle-size selection experiments. In these, the experimental setup was the same but all seven containers used had unsorted material of the same particle-size range (95.27% within the 125 - 1000 μ range) taken from Salmon Cove and incinerated at 600°C. for 20 hours. All material was of the same color.

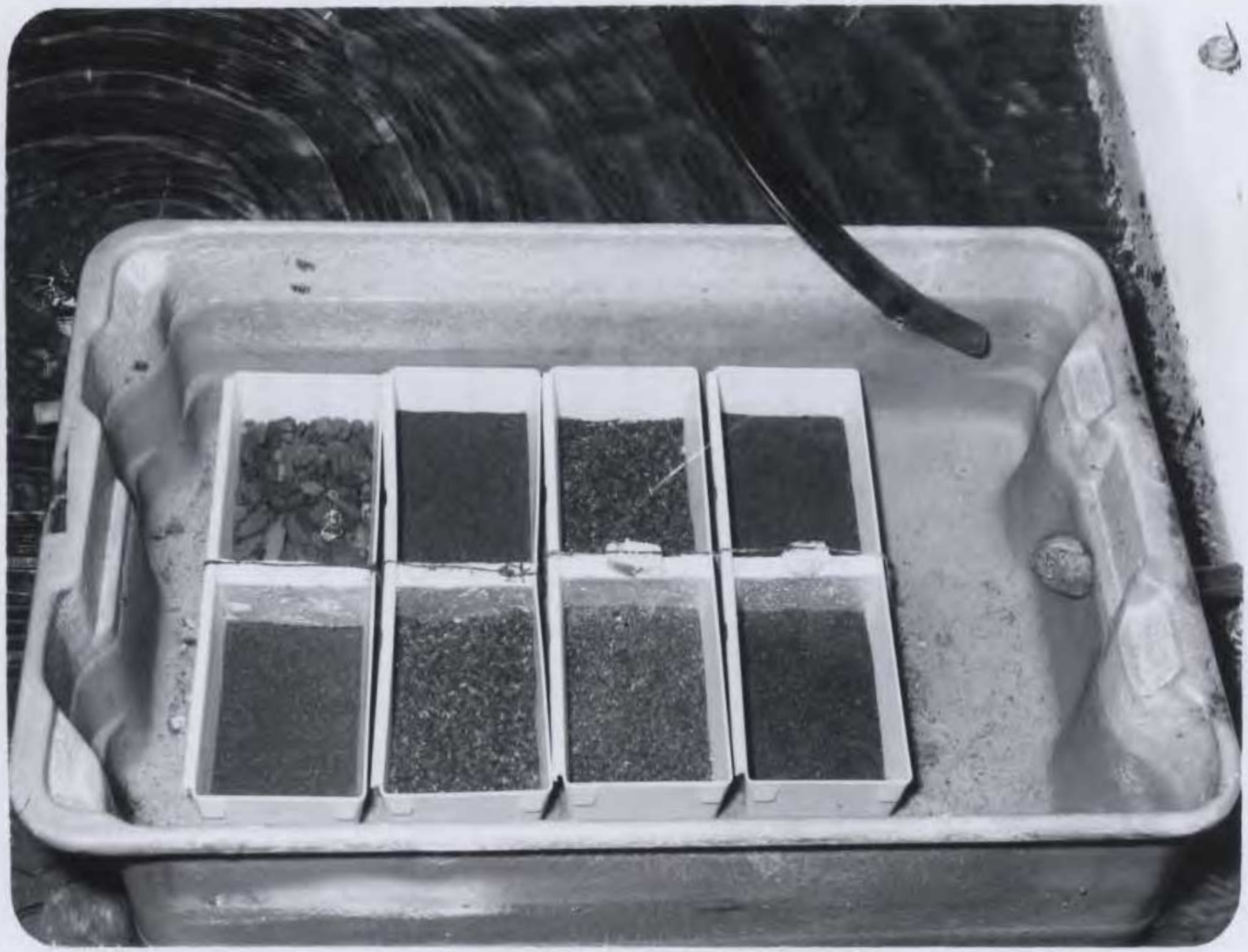
Each control had 140 animals and ran for 22 hours. They were conducted during the period August 2 - 6, 1971.

2. Particle Size

Plate 8 shows the experimental setup for the first series of substrate particle-size selection experiments conducted on August 2-6, 1971. Table 4 gives the substrate particle-size range offered in each container compartment (containers No. 1-7 only in the table). The containers were 22.5 cm. long, 7.2 cm. wide and 4.8 cm. high; divided

Plate 8.

Experimental setup for particle-size substrate selection experiments.



into two equal compartments by styrofoam partitions; and filled to a depth of 2.5 cm. with substrate. The containers were divided because of the difficulty in acquiring sufficient quantities of pre-determined particle-size ranges. These were submerged in one holding tank and supplied with running seawater.

All the substrate used came from Salmon Cove and was incinerated at 600°C for 20 hours.

In each experiment 140 animals were dropped onto the water surface above the particle-size choices and were left for 22 hours after which the substrate in each container was sieved, the animals removed and counted. Animals which had not made a choice of substrate but were found inside the holding tank were also counted.

Five control experiments used also in conjunction with the substrate color selection experiments have been described in the previous section.

In the second series of seven experiments on particle-size selection the set up was the same (Plate 8). These were conducted July 12-18, 1971. All the substrate used came from Salmon Cove as before but it was dried at 60°C. for 20 hours instead of being incinerated.

Each compartment was filled with substrate of the particle-size ranges given in Table 4 and, because of the increased number of containers, placed in two holding tanks each of which received an equal number of containers. Both were supplied with running seawater and in every respect could be treated as one large holding tank.

In each experiment 280 animals (140 to each holding tank) were dropped onto the water surface as before and left for 22 hours after

which the number of animals in each compartment was determined by sieving. Animals found outside the substrate choices were counted as before.

Five control experiments were conducted in conjunction with the second series. The experimental setup was the same as in the second series but each of the seven compartments used had unsorted material of the same particle-size range (95.27% within the 125 - 1000 μ range) taken from Salmon Cove and dried at 60°C. for 20 hours.

In each control 140 animals were used and each ran for 22 hours. All control experiments were conducted August 6 - 10, 1971.

IV RESULTS

A.

1. Salmon Cove

(a) Physical and Chemical Factors

i Temperature

Range of temperatures throughout the year at Salmon Cove for both the seawater and the substrate was - 1.0 -- 15.0°C. (Appendix 1a). Mean temperature for thirteen months for the seawater was 4.89°C and mean temperature for the substrate was 4.78°C.

Temperature of both the seawater and the substrate decreased during the fall of 1970 and winter of 1971 to a minimum of - 1.0°C in January (Fig. 5a). There was a steady rise after February to a maximum of 15.0°C in September but a decline again in the fall.

ii Salinity

The salinity range of the seawater throughout the year at Salmon Cove was 17.8 - 31.6 ppt (Appendix 1a). Mean salinity for thirteen months was 28.37 ppt.

Considerable fluctuations occurred during the fall of 1970 and from January to early May, 1971 (Fig. 5b). Since the seawater samples were generally taken at monthly intervals, heavy rain or a prolonged dry period could have effected these changes. Monthly seawater salinities remained relatively uniform decreasing gradually from 31.5 ppt to 28.6 ppt. between May and December.

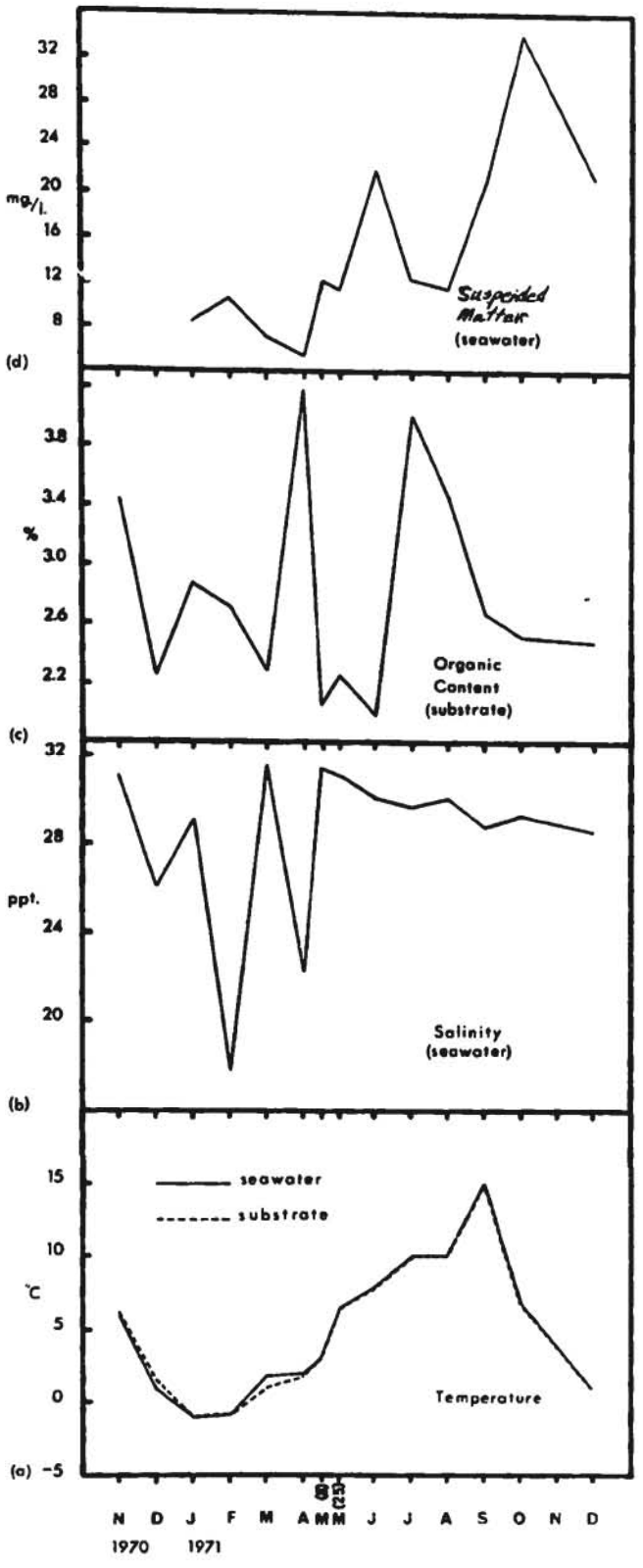


Fig. 5. Physical and chemical factors at Salmon Cove.

iii Organic Content of the Substrate

Range in the monthly per cent of organic material present in the substrate at Salmon Cove was 1.99 - 4.19% (Appendix 1b). Mean for thirteen months was 2.80%.

A decrease in the amount of material present in the substrate is evident in the winter months (Fig. 5c). It did not rise above 2.87% from December, 1970, to March, 1971 (Appendix 1b). There was a sharp rise to a maximum for the year of 4.19% in April but a decrease in May to a minimum for the year of 1.99% in June. Organic material in the substrate reached another peak in July but gradually declined until December when sampling ceased.

iv Suspended Matter in the Seawater

Range in the suspended matter present in the seawater throughout the year at Salmon Cove was 5.4 - 34.2 mg./l. (Appendix 1b). Mean for eleven months was 14.76 mg./l.

Although no 1970 fall samples were collected for this parameter, the low winter values are again evident (Fig. 5d). These continued throughout the winter and spring to a minimum for the year of 5.4 mg./l in April (Appendix 1b). There was an increase through May to a low peak in June. This is quite the reverse of that for organic content of substrate since a minimum low for the year was recorded for this month.

Organic content of the seawater decreased and remained low during July and August but an increase which began in September culminated in a maximum for the year of 34.2 mg./l. in October (Fig. 5d). A decrease

during the winter was evident from the December sample but the value of 21.3 mg./l recorded was again relatively high (Appendix 1b).

v Substrate Composition

Appendix 1c and Fig. 6 show that 51.1% of the substrate by weight at Salmon Cove (mean of samples taken at stations No. 1, 3 and 5) falls within the particle-size range of 125 - 250 μ. A total of 82.54% falls within the 125 - 250 μ range and 95.27% is within the 125 - 1000 μ range. An insignificant amount is outside the upper and lower limit of the 125 - 1000 μ range.

(b) Distribution at Salmon Cove

i Depth Distribution

From somewhat limited sampling done at Salmon Cove during the last week in May a concentration of animals was found at a point 25 meters from the HWS line going outwards perpendicular to the shoreline (Fig. 2 and 7 and Table 7).and approximately 18 m. from LWS.

The 25 meter point is located near the level of five temporary stations established at Salmon Cove in October, 1970, and sampled throughout the year (Fig. 2). An abundance of animals occurred at this point particularly in the summer and fall in the regular monthly samples. Since very few animals were taken seaward of this point at 50, 75 and 100 meters from HWS in water depths of 1.5 - 3.0 m., it is likely that there is a band of concentration of *Amphiporeia lawrenciana* 25 m. from HWS during the warmer months. No animals were taken landward of this point.

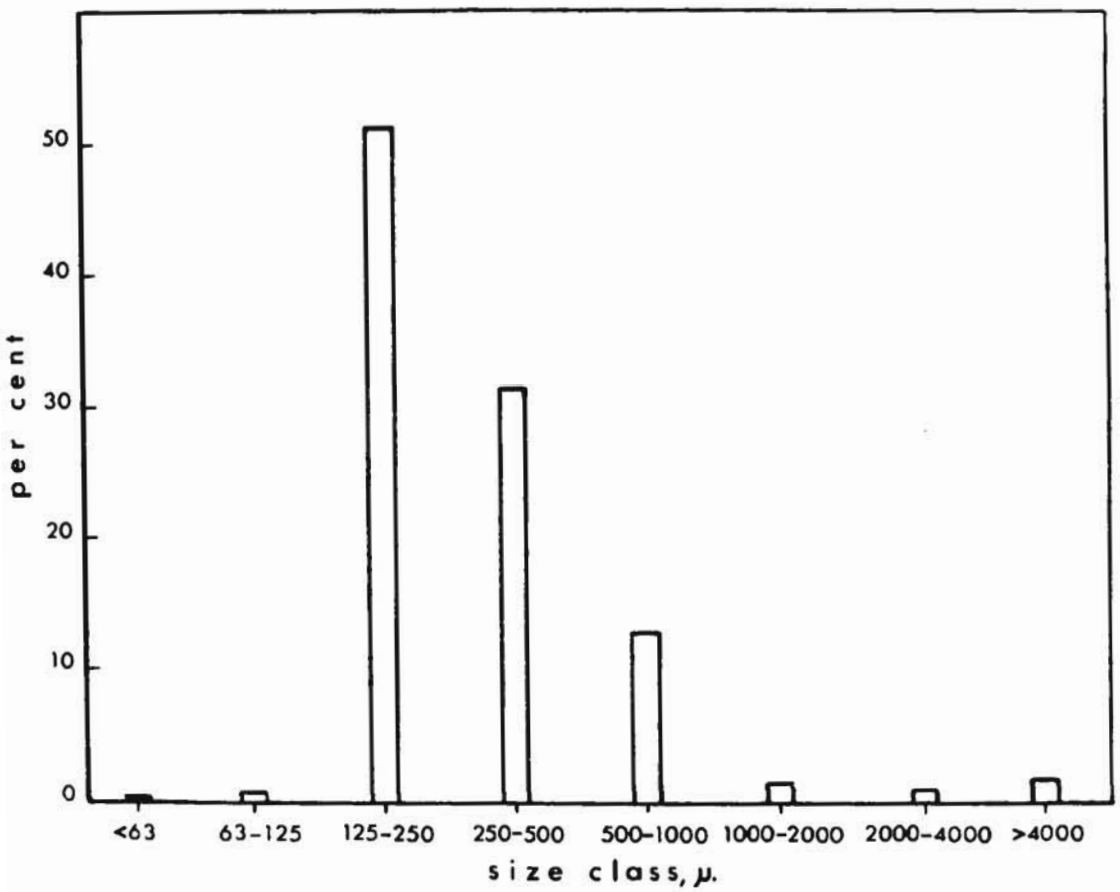


Fig. 6. Per cent particle-size composition (average weight, mg., of five samples) of the substrate at Salmon Cove.

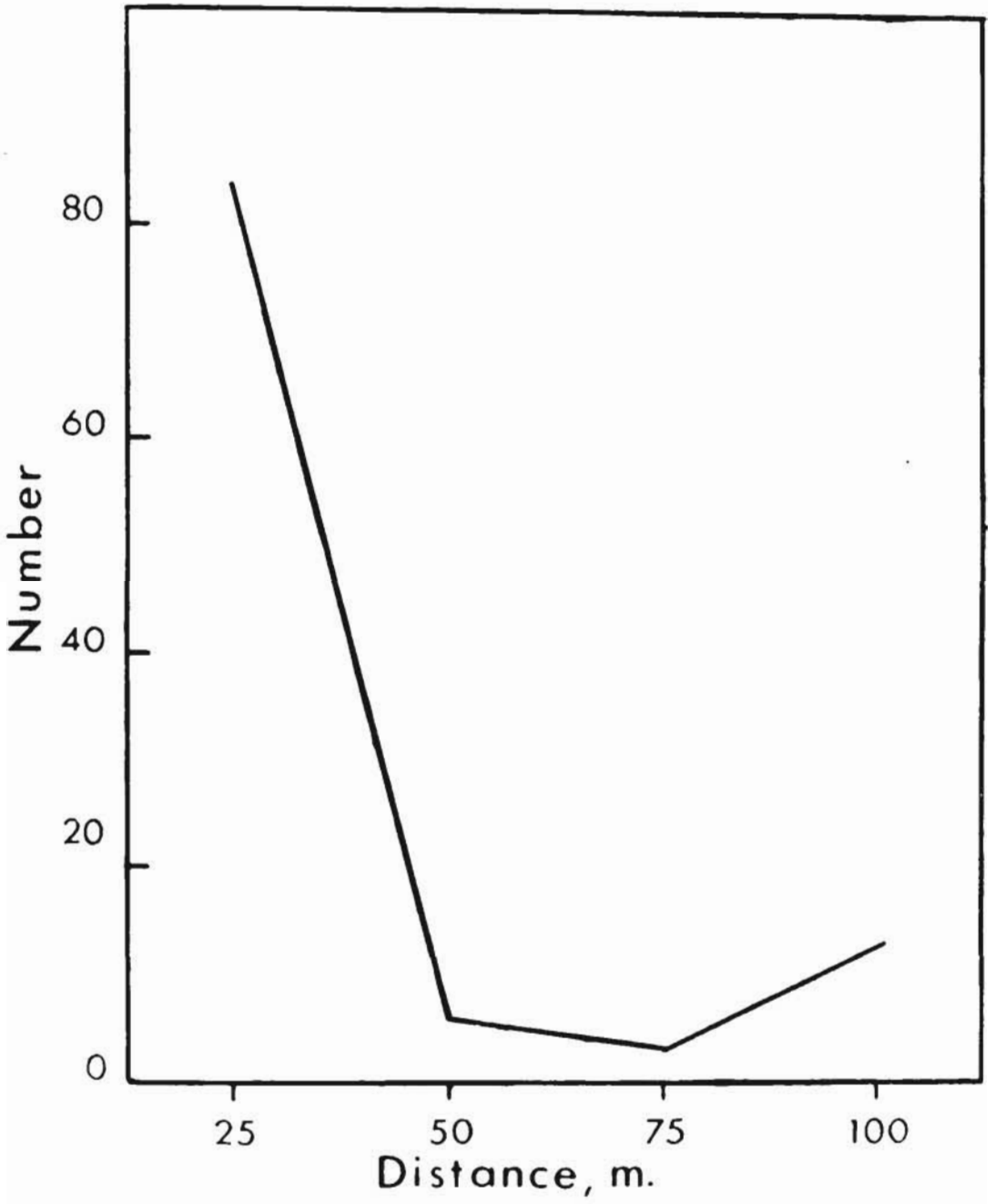


Fig. 7. Number of animals per 0.1m.^{2} taken at 25-meter intervals from HWS (the 0-meter point).

Table 7

Number of animals per 0.1 $m.^2$ sample collected at intervals from the HWS line (0 meter point)

Distance from HWS, m.	Water Depth, m.	Animal length, mm.								Number/ 0.1 $m.^2$
		5	6	7	8	9	10	11	12	
25	0.5	6	14	10	24	21	6	2	1	84
50	1.0	-	2	2	2	-	-	-	-	6
75	2.0	1	1	1	-	-	-	-	-	3
100	3.0	4	5	-	2	2	-	-	-	13
	Total	11	22	13	28	23	6	2	1	106

ii Vertical Distribution

Appendix 2 shows that the mean depth burrowed by the 33 animals observed was 6.59 mm. Range of depths burrowed was 2.5 - 15.0 mm. Range of lengths of the animals observed was 6.5 - 10.0 mm.; the mean length was 8.12 mm.

It was found that if the animals encountered difficulty in penetrating the substrate they would remain for varying lengths of time with the posterior end protruding from the sand. While burrowing beneath the surface of the substrate, their pleopod beat continued with no apparent decrease in frequency compared to that at the surface. This observation was made on two occasions while the animals burrowed close to the side of the observation chamber.

Fig. 8 shows the regression line of the animal length plotted against depth burrowed ($\hat{y} = 1.91X - 9.43$). A correlation exists between length of the animal and the depth it burrows into the substrate.

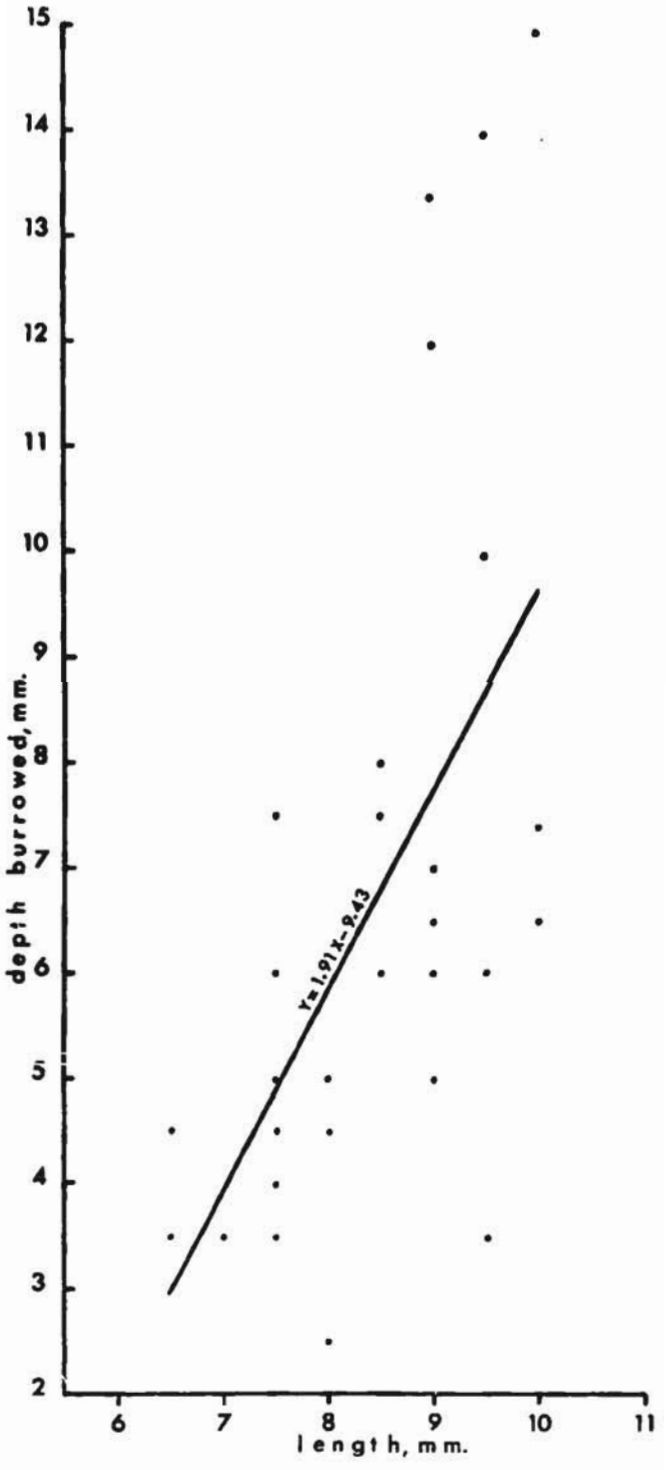


Fig. 8. Body length--depth burrowed relationship for *A. lawrenciana*.

Temperature of the water was maintained as closely as possible to 15°C in the observation chamber during these measurements since it was found that, when it reached 17°C, the animals became sluggish and ceased to burrow. This was accomplished by siphoning at intervals from the observation chamber and replacement from the running seawater system.

(c) Reproduction

i Coloration

Male *A. lawrenciana* maintain the same body color throughout the year; females change their color during reproductive periods.

The most obvious change is the darkening of the dorsum and brood pouch areas caused by swollen purple ovaries which are visible through the body wall prior to embryo deposition into the brood pouch and during the period of embryonic development. Faint orange patches which are found at the anterior and posterior ends of the animal become brilliant orange and very conspicuous when the female enters the reproductive phase of the life cycle. This is particularly true for the posterior region. A light yellow-orange color also appears dorsally near the mid-line in gravid females. Quite apart from the larger size, females are easily distinguished on the basis of body color from males at this time even without a microscope. A female with late C- or D- stage embryos in the brood case is very conspicuous. The orange-colored embryos with dark-brown yolks are clearly visible through the coxal plates (Plate 9).

Plate 9.

Amphiporeia lawrenciana: female with D-stage embryos.

D-stage embryo.

yellow coloration at the mid-line.

developing ovary.

ii Reproductive Behaviour

The "carrying" habit characteristic of "primitive" gammarids in precopula is thought to have been lost in more advanced haustoriids although the slightly enlarged gnathopods still persist in *Amphiporeia lawrenciana* and other more "advanced" forms (Bousfield 1970). Precopulae or attempts by the males (6 - 8 mm.) to carry the much larger females (10 - 12 mm.) were observed in this species on four separate occasions.

The first of these occurred in mid-March while the others took place on April 26, April 27 and June 8 respectively. One observation was made in the field shortly after live animals had been collected; the others occurred inside holding tanks at the laboratory shortly after live animals had been brought from the field.

The behaviour pattern on each occasion was the same. The female lay passively on her side while the male attached himself firmly between the thoracic plates immediately posterior to the head. In this position he curled his body in towards the female until the ventral surfaces appeared to touch. Although the position prevented good observation of exactly how the attachment was made, it is likely that the gnathopods were engaged.

The male, once attached, attempted to move the larger female. He was unsuccessful but some movement did occur when the female dug her uropods and telson into the substrate and extended the body.

Longest period of observation was ten minutes at the laboratory. It probably would have continued had an attempt not been made to examine the activity microscopically. The animals separated and swam away appearing to lose interest in each other; pairing activity did not

resume although they were observed for more than an hour afterwards.

It is believed that what was observed on these occasions was not precopula behavior but the act of copulation itself. Kinné (1956) has sketched and described copulation in *Gammarus duebeni*. Positions of the male and female in his sketch are almost identical to those observed for *Amphiporeia lawrenciana*.

iii Embryo Size

Table 2 shows that mean size for embryos of the A-stage sample was 0.829 mm. (range = 0.700 - 0.950 mm., S.E. = 0.018 mm.). There was a progressive increase in the mean sizes of embryos of each sample examined from A-stage through B, C and D stages up to hatched young which had a mean size of 1.389 mm. (range = 0.900 - 1.650 mm., S.E. = 0.145 mm.).

Since all specimens were preserved in 70% alcohol, it is likely that the mean sizes for embryos given are somewhat lower than those for live animals.

iv Fecundity

Figure 9 compares the number of oogonia with female body length (Table 8) and the number of embryos found in the brood pouch with body length (Table 9). Oogonia line has been shifted 1 mm. to allow for growth of the oogonia.

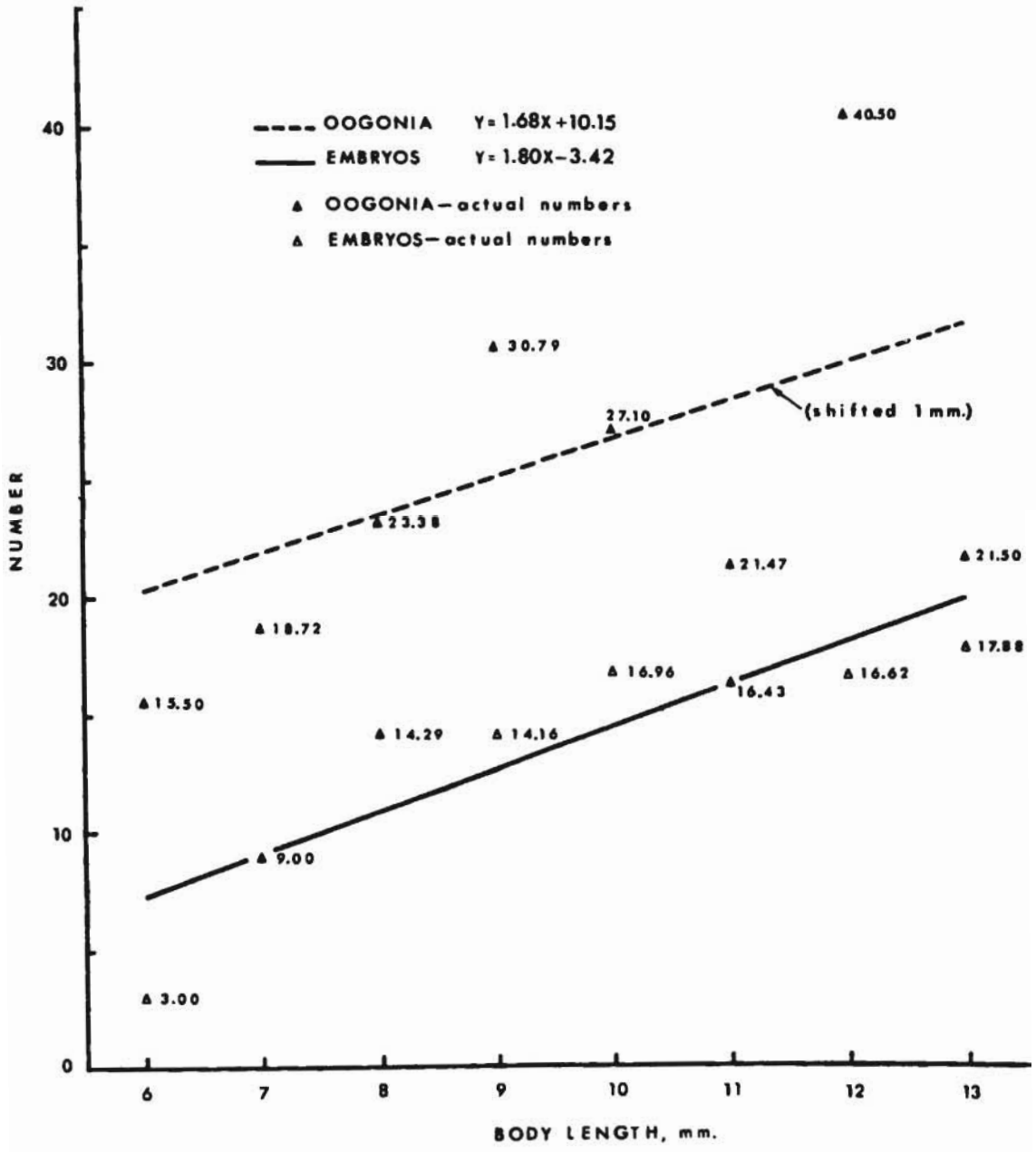


Fig. 9. Number of oogonia and embryos per female at Salmon Cove. Actual means are given on the graph.

Table 8

Mean Number of Oogonia and Oocytes* Produced by Female *A. lawrenciana* per length class

Length, mm.	Number of animals	Number of oogonia	Mean number per female
6	4	62	15.50
7	36	674	18.72
8	55	1286	23.38
9	72	2217	30.79
10	58	1572	27.10
11	34	730	21.47
12	18	729	40.50
13	8	172	21.50

*All egg stages in the ovary are referred to as oogonia in the text.

Table 9

Mean number of embryos carried by female *A. lawrenciana*

Length, mm.	Number of animals	Number of embryos	Mean number per female
6	23	69	3.00
7	66	594	9.00
8	77	1100	14.29
9	102	1444	14.16
10	73	1238	16.96
11	40	657	16.43
12	26	432	16.62
13	8	143	17.88

Slope of the two lines is approximately the same indicating that the increase in oogonia and embryo numbers with animal length is similar (Fig. 9). The slope of the line in each case is low, however, indicating that the increase in numbers with body length is not great. The number of embryos is significantly less than the number of oogonia per female. One explanation for this might be that a considerable number of ova do not develop.

v Reproductive Cycle

Figure 10 and Appendix 3 give the stages of oogonia and embryos for the year for the Salmon Cove population. In October 15% of the oogonia of females had enlarged. A-stage embryos were found only in two females in December and February. These probably represent the early beginning of the reproductive period for a few animals. In March the first significant number of A-stage embryos were found in brood pouches. There follows then, apparently, a relatively long embryo development period since hatched young were not found in the samples until May, more than two months later.

Young are released from May to August with the bulk in August when the largest number of females with long setae and empty brood pouches were obtained.

End of the reproductive cycle occurred in August when practically all of the oogonia in samples were in class 1 and there was a marked decrease or complete absence of A, B and C- stage embryos but a relatively high percentage of D- stage embryos in the brood pouches.

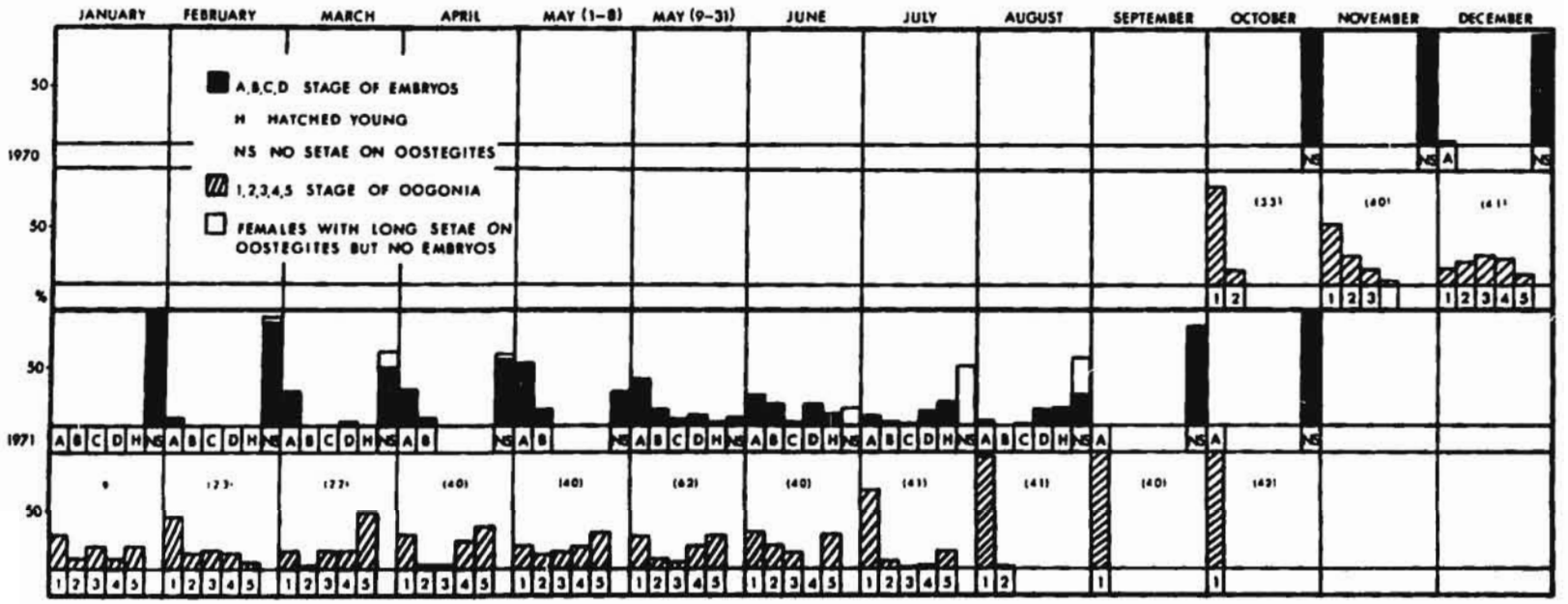


Fig. 10. Stages of embryos and oogonia. Numbers of animals examined are given in brackets with the oogonia.

vi Number of Broods Per Year

Plate 9 shows a female with D-stage embryos in the brood case and well-developed purple ovaries as well. A number of animals were observed in this condition from April through to July. It is a good indication that at least two broods of young are produced per year.

Fig. 10 shows that only in the months of August, September and October were close to 100% of the oogonia in class 1. Although a few females carried embryos in the brood pouches in December and February, it was not until April and May that large numbers were deposited in brood pouches. It was found that during these months many of the females carrying C and D- stage embryos also had oogonia in the early stages of development. This second brood of embyros is probably deposited in the brood pouches in June and released as young sometime in the fall. It is difficult to say exactly when these events occur for the second brood of young since the effect on the general population overlaps that of the first brood. The relatively long period in which young in the lower length ranges continue to appear in monthly samples (June to September) suggests that two broods, or even three, are produced by *A. lawrenciana*.

(d) Abundance

Samples show that the population is at its peak at Salmon Cove at the level of the temporary stations (Fig. 2) in October and at its lowest point in January (Appendix 4a and Fig. 11). The relatively small number taken in the sample of October, 1970, is not considered to be representative of the actual population, because many animals were lost in this initial collection.

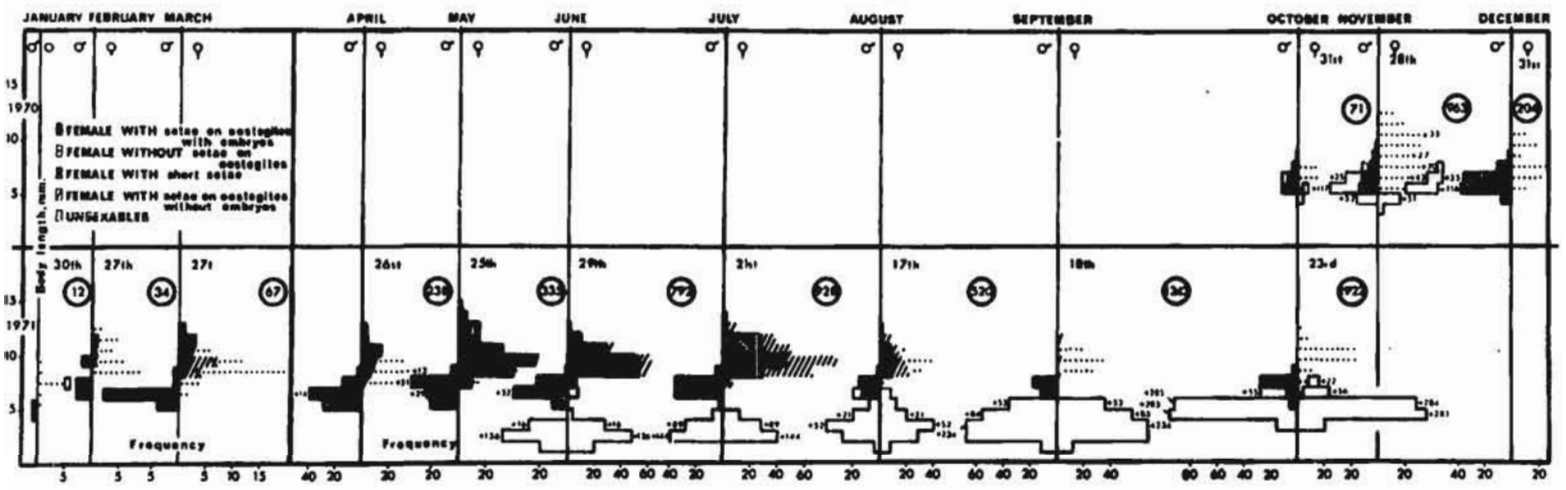


Fig. 11. Size compositions of *Amphiporeia lawrenciana* collections. Number of specimens examined per month are shown in circles.

The total population is lowest during January, February and March. Samples show that there is a rapid increase in April which continues throughout the summer and fall to reach a peak in October with heavy recruitment from the new generation (Appendix 4f and Fig. 11). Fall collections show that the population decreases rapidly through November and December.

Figure 12d shows that males have two peaks in abundance (Appendix 4b): one in December and one in May. An interesting comparison can be made between this and the females. Females without setae on the oostegites reach three peaks of abundance: in April; in October and the largest in November (Fig. 12c). The April and November peaks occur one month before the peaks in male abundance. The winter decrease, which affects both sexes, begins a month later for the males. The April peak for females without setae on the oostegites is low since many are becoming ovigerous at this time.

Significant numbers of ovigerous females occur only between April and August (Fig. 12c and Appendix 4d). It is during this period that practically all of the adult females reproduce and release young beginning in June (Fig. 12b and Appendix 4f). Only one female out of a total of 246 taken in the July collection was without long setae on the oostegites.

Females with long setae on the oostegites and without embryos were in good number in July only. Many of the females release young at this time as the population is nearing the end of its reproductive period and the older animals are at the end of their life cycle.

Between June and October the population size is determined by

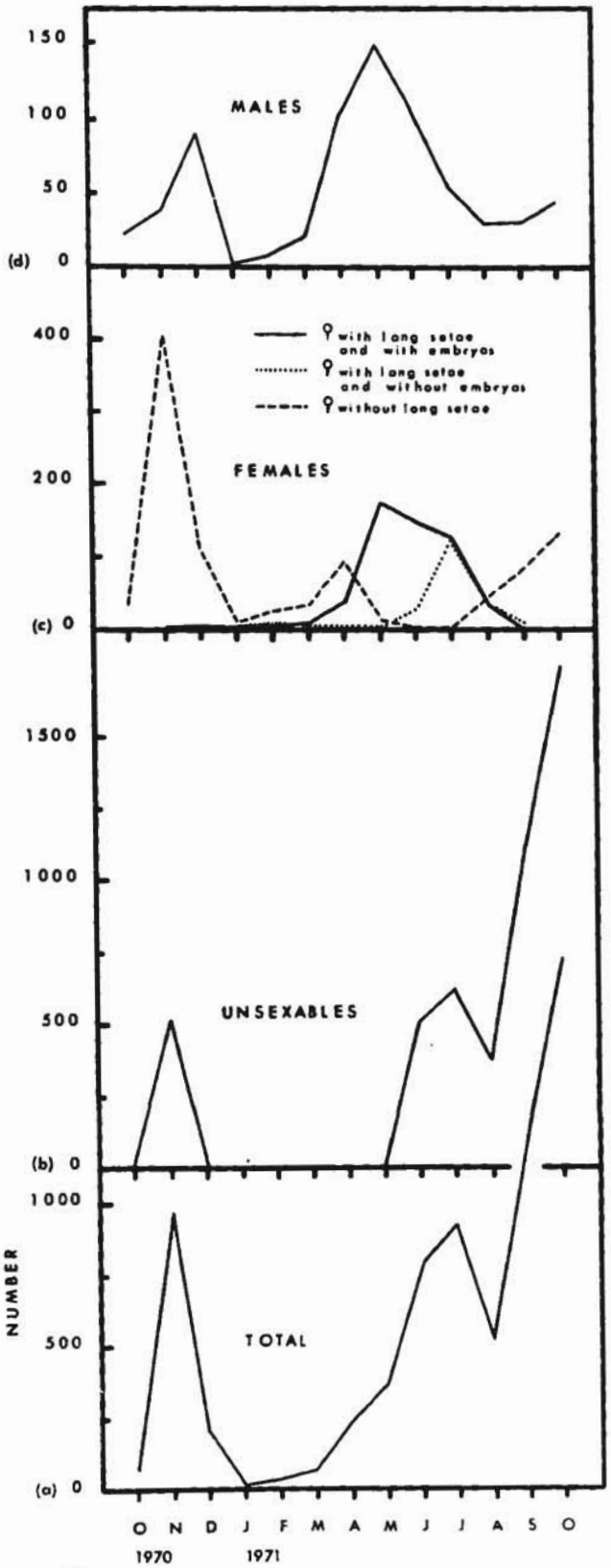


Fig. 12. Monthly number of animals present in the samples taken at Salmon Cove.

the new generation of recruits referred to as unsexables (Fig. 12b and Appendix 4f). In these months large numbers of young are released as indicated by the fact that the samples are dominated by them. In the month of October, for example, when the population reaches its peak, 90% of the sample consisted of unsexables (Appendix 1 and 6).

It is significant that the unsexables disappear from the samples after November passing for two reasons: first, the unsexable animals soon develop sexual characteristics and are thereafter classed as male or female; second, at the beginning of winter they may move offshore early or possibly burrow deeply into the substrate.

2. Other Areas

a) Collections

Amphiporeia lawrenciana were found at 8 of the 29 beaches sampled in Newfoundland during the summer of 1971 (Table 10). No animals were found at other locations.

Table 10

Numbers of *Amphiporeia lawrenciana* collected in Newfoundland

Beach Number	Beach	No. of Animals/0.1 m.^{2}
1*	Windmill Bight	319
2	Southern Brook	64
3	Deadman's Bay	93
21	Indian Island	115
22	Sandy Cove	59
24	Port Saunders	32
27	Shoal Cove	7
28	Portland Creek	3

* See Fig. 3.

b) Physical Factors

A summary of the parameters temperature (seawater and substrate), salinity and suspended matter (seawater) for the 29 beaches sampled in Newfoundland during the summer of 1971 (Fig. 3) is given in Appendix 5a. Substrate particle size composition is given in Appendix 5b.

Table 11 gives the ranges and means for temperature, salinity and suspended matter of the seawater for beaches sampled in Newfoundland.

Table 11

Ranges and means of temperature, salinity and suspended matter at beaches in Newfoundland

Parameter	Beaches where *A. lawrenciana* were found		Beaches where *A. lawrenciana* were absent	
	Range	Mean	Range	Mean
Temp. Seawater, °C.	7.8-19.0	13.1	12.7-24.0	15.7
Temp. Substrate, °C.	8.8-17.5	13.3	12.0-21.0	14.7
Salinity, ppt.	5.0-30.2	20.7	6.2-29.5	23.4
Suspended matter, seawater, mg./l.	2.0-64.4	22.1	8.6-40.2	16.8

Table 12 gives the percentage of the substrate within the 125 - 1000 μ range (the range within which 95.27% of the substrate at Salmon Cove falls) for exposed and protected beaches sampled in Newfoundland. The beaches where *A. lawrenciana* was collected have been indicated. No particle-size range is given for Shoal Cove (Fig. 3 - No. 27) since the sample was lost.

Table 12

Percentages of substrate at exposed and protected beaches within the 125-1000 μ particle-size range.

Exposed		Protected	
Beach Number	Substrate per cent in the 125-1000 μ range	Beach Number	Substrate per cent in the 125-1000 μ range
1*	92.23	4	35.55
2*	83.95	7	59.62
3*	94.66	8	50.39
5	54.99	10	58.91
6	15.40	11	56.67
9	64.63	12	55.79
17	61.68	13	84.45
18	36.59	14	67.34
20B	75.18	15	2.33
21*	97.70	16	64.85
22*	97.47	19B	66.24
23	25.41	20A	92.10
24*	55.34	25	48.33
26	50.64		
28*	48.93		
29	55.12		

* Beaches at which *A. lawrenciana* were collected.

3. Length-Weight Relationship

Figure 13 shows that the increase in weight with length is considerably greater for the females than for the males for preserved animals (70% alcohol). Samples used for this analysis were all collected in late May, when females of 8 mm. and longer were ovigerous, and analysed one week later. Actual length-weight values for females

of length 5 - 7 mm. closely approximate the slope of the regression for males of the same length range (Fig. 13). As one would expect, ovigerous females are apparently much heavier while they are carrying embryos at various stages of development in their brood cases.

Regression line equations are $y = 3.66x - 20.29$ for the females and $y = 1.62x - 8.15$ for the males (where y = weight and x = length).

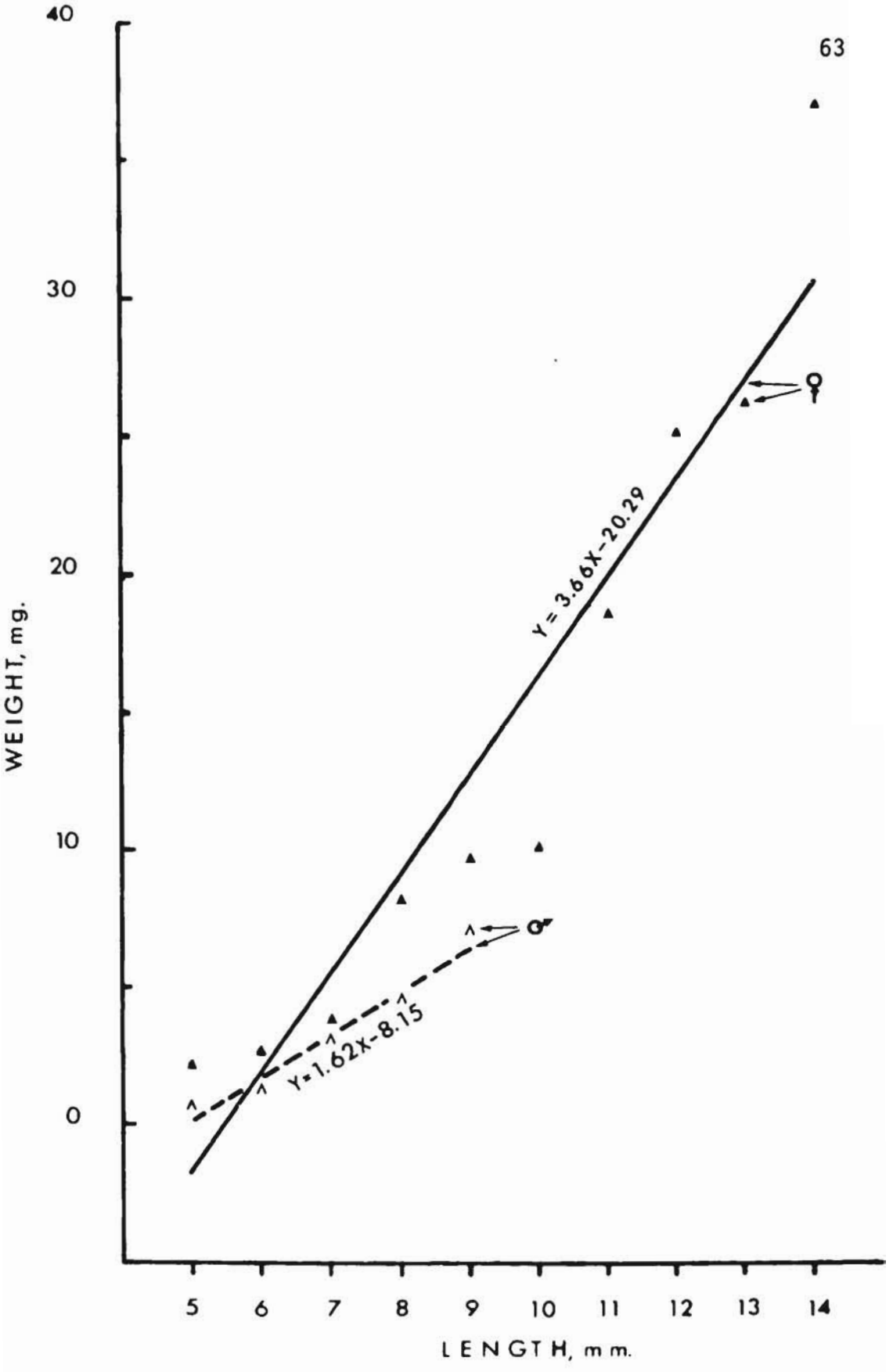


Fig. 13. Length-weight relationship of male and female *A. lawrenciana* taken at Salmon Cove.

B.

1. Functional Morphology

a. Swimming

Amphiporeia usually swims at an angle of approximately 35° to the horizontal (Fig. 14). The metachronial beat of three pairs of pleopods is responsible for steady, powerful, backwardly-directed water currents which result in forward motion of the animal.

Water moves toward the head and cephalo-thoracic region from the front and from all sides (Fig. 14). The streams are drawn up toward the oral surface and meet near the mid-line at about the level of the mouth where the feeding current resulting from movement of maxilla 2 branches off (page- 71). One broad stream continues posteriorly within the partially enclosed tunnel created by the coxal plates and is joined by water moving in from both sides over the ends of these plates (Fig. 15).

This current is joined by two strong currents forming the edges of two broad vortices of water entering between the coxal plates (Fig. 15). At this point the current formed by water from three directions rises closer to the ventral surface in the region of peraeopod 3, 4 and 5 (Fig. 14); it then moves rapidly away from the body as it comes close to the pleopods (Fig. 15).

Rapid movement of the current away from the posterior end of the body provides the motive force for forward movement. A considerable volume of water moving away, splits to form the posterior parts of the two vortices of water mentioned (Fig. 15); the influence of these on the

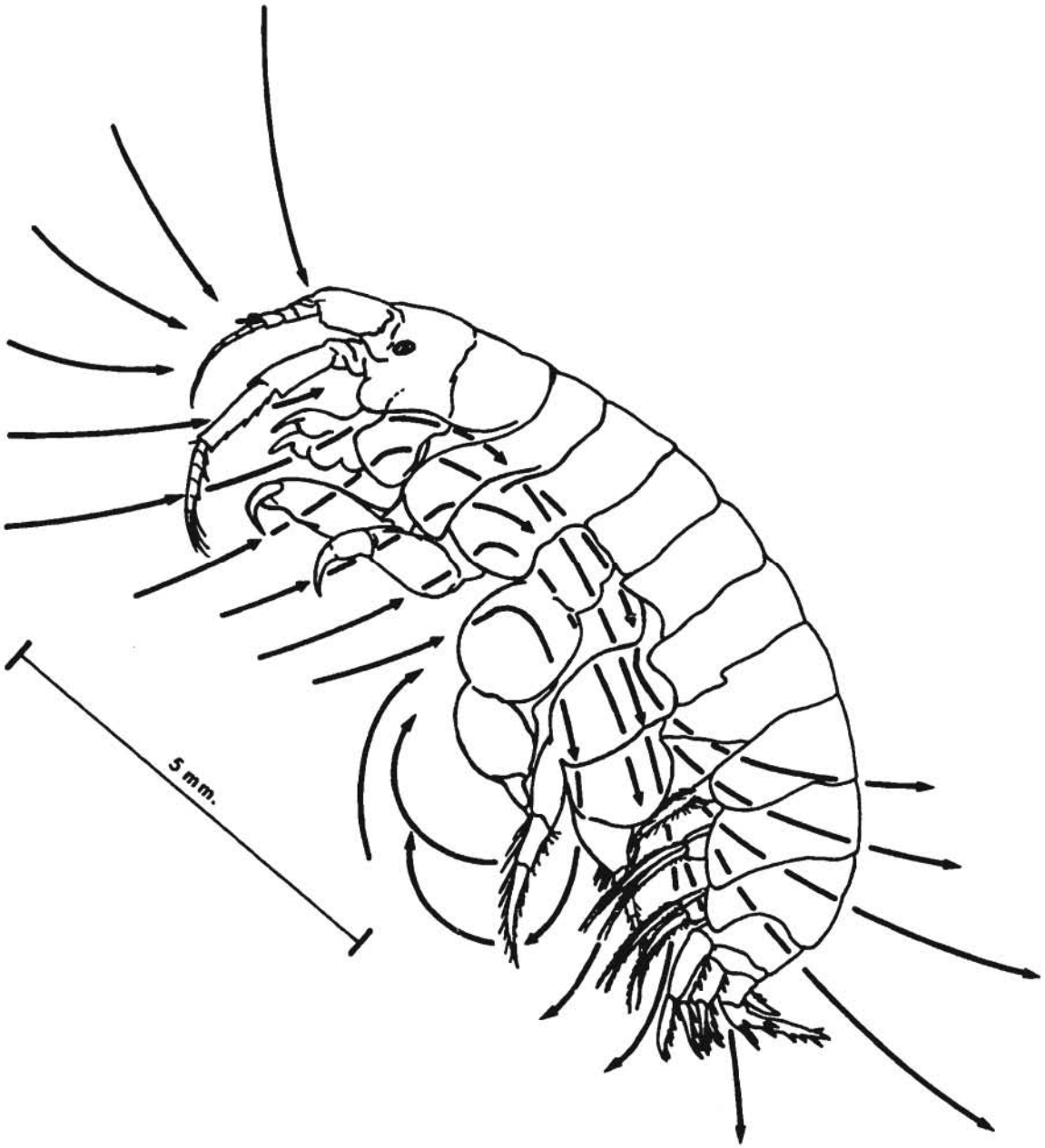


Fig. 14. Side-view of *A. lawrenciana* showing body orientation while swimming and water currents.

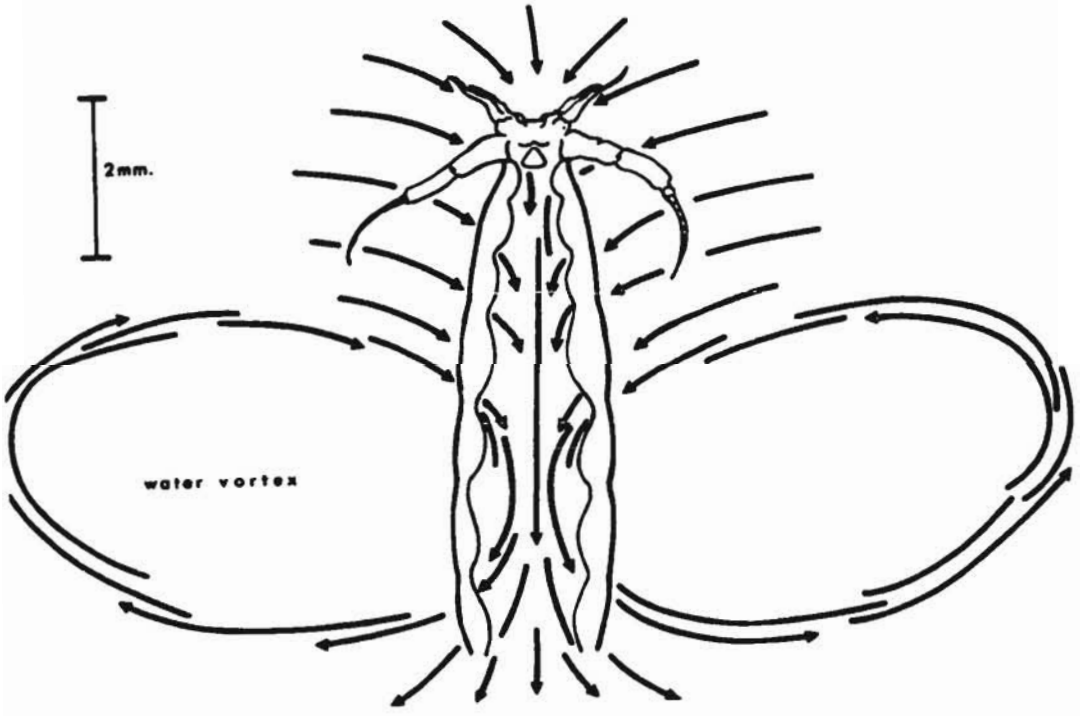


Fig. 15. Front view of *A. lawrenciana* showing water currents.

surrounding water can be seen as far away as 8 mm. from the sides of a large animal. The two currents flow out between the coxal plates.

The vortices appear to be more compact than the general body current proceeding posteriorly. They appear to be moving faster and to be carrying a greater volume of detritus from the surrounding water. Some of this material is lost from the vortices as they move towards the anterior in their outer margins and recirculates along the body with water approaching the head region.

Pleopods 1, 2 and 3, which are responsible for the water currents, are biramous. The positions of the rami on the forward and backward strokes are similar to the description given by Dennell (1933) for *Haustorius*. The two rami of each pleopod open on the backward stroke and the setae extend laterally to provide maximal water resistance. Coupling hooks on the inside surface of each pleopod probably lock each pair together during the backward stroke thus ensuring that their strokes are in unison. Since the outside marginal setae on the rami of the third pleopod pair are relatively long, this adds power to the backwardly directed current. Setae are fully extended near the mid-point of the backward stroke but they gradually collapse near the end.

The rami close at the beginning of the forward stroke and the setae collapse fully and stream loosely behind. The rami then move forward with minimal water resistance. The setae begin to extend laterally again near the end of the forward stroke.

The animal usually exerts short bursts of speed to the surface where swimming ceases and it sinks slowly down to the bottom.

Extension and flexion of the body, which aid the main propulsive force, are responsible for these bursts of speed. The effect is to make *Amphiporeia* a clumsy and awkward-looking swimmer. Occasionally one animal swam the complete length of the holding tank (approx. 60 cm.) without stopping but most simply swam up to the water surface and sank.

Most swimming occurred after the animals had been disturbed or for well over an hour after they had been brought from the field. It was found by observation at the laboratory that, for animals brought recently from the field, periods of most active swimming corresponded with night high tide. A series of hourly plankton tows at Salmon Cove showed a similar periodicity. This was true particularly for the males.

b. Burrowing

In the first stage of burrowing the body is held rigid and slightly extended. The animal swims rapidly toward the sand and, since a rostrum is absent in the species, the peduncle of antenna 2, with the flagellum deflected, acts as a kind of spear to aid initial entry. Basal joints of antenna 2 deflect sand grains to the side as the animal burrows. Occasional flexion and extension of the body has the effect of settling it into the sand.

Once entry is effected, water currents expel sand grains to the rear and sides. The two swimming vortices and the main water current provide considerable propulsive force. These currents together with efficient mechanical action make *Amphiporeia* an effective and rapid burrower.

All animals burrow a short distance before coming to rest; a

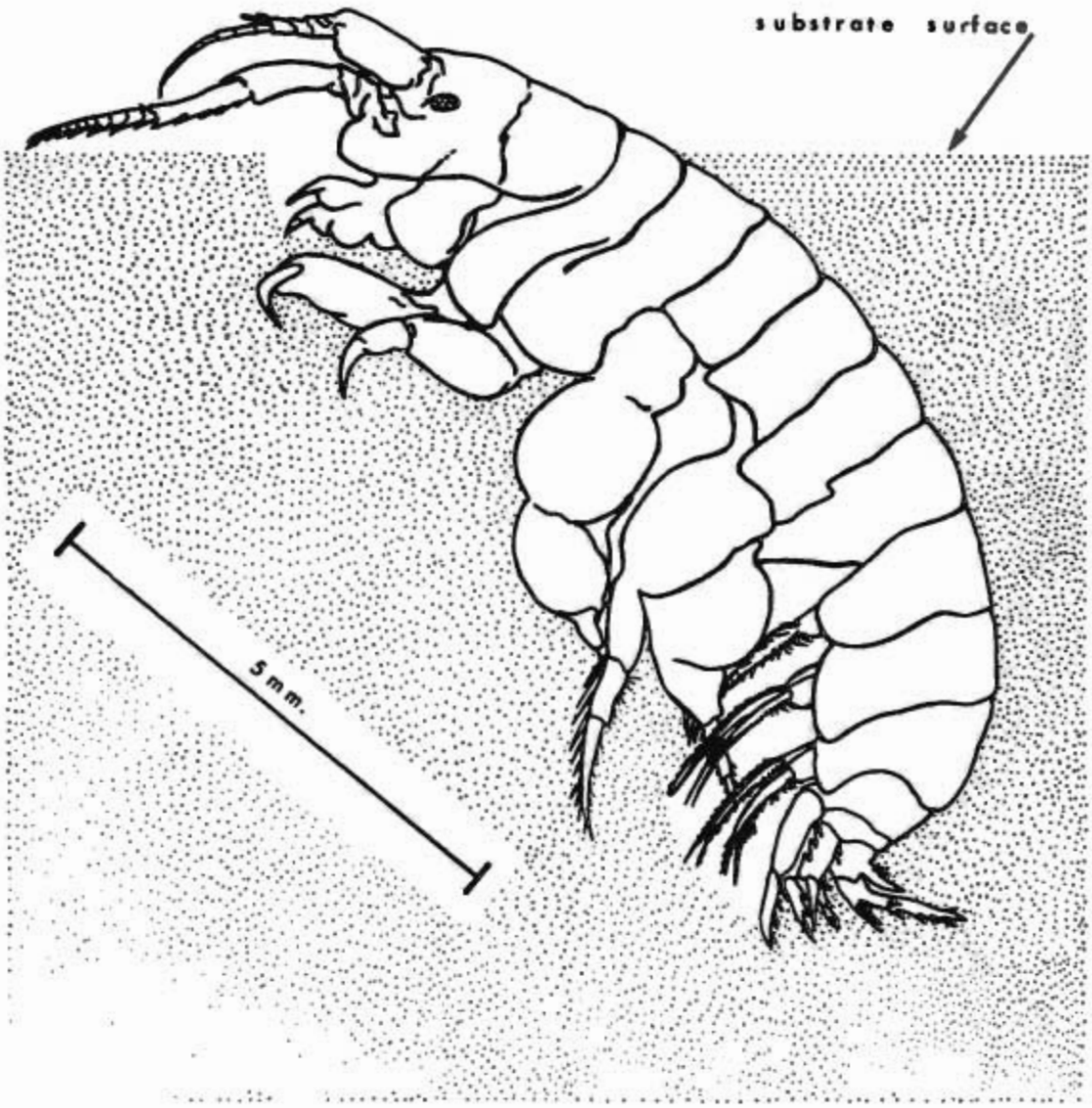


Fig. 16. Body orientation in the substrate after burrowing has ceased.

few were observed to leave furrows in the sand up to 20 cm. in length in one night (page- 72). It is likely that these represent a series of short burrowing spurts rather than one long period.

Culmination of burrowing for most animals occurs shortly after entry when the head is pushed out of the sand and thus comes to rest at an angle of approximately 35° from the horizontal, the same angle used in swimming (Fig. 16). The pleopods continue to function and water currents move towards the head in the same way as in swimming. The animals apparently feed and the gills acquire oxygen from the circulating water in this position.

There is some difference in the vigor with which different animals burrow. Burrowing action continued for most animals when they were placed in a dish with no sand. Even when the water temperature approached the lethal limit and long after they had ceased swimming, many animals continued their attempts to burrow.

A few animals could not be dislodged from the sand even with a strong jet of water; others emerged at the slightest disturbance.

2. Feeding

a) Feeding Habits

i. Behavior

Limited observations on the behavior of *Amphiporeia lawrenciana* while feeding have shown that in the "resting" position described following burrowing activity (Fig. 16), filter feeding takes place. While the animal lies *in situ*, normal water currents continue since

the pleopod beat is maintained. Observations using iodine-stained starch granules indicate that suction from movements of maxilla 2 creates a small but effective feeding current. Only a small portion of the total number of granules approaching in the normal water current actually are drawn into the feeding current; the remainder continue posteriorly.

Floculant masses of starch which became entangled in the mouthparts were quickly thrown out by rapid movement of the mandibular palps. Only the smaller particles continued to the maxilla 2 filtration apparatus. As in *Haustorius* (Dennell 1933), the endite and exopodite of maxilla 2 are absent and the dense setation of the two remaining lobes (inner and external) act as an efficient sieve as well as a suction pump in filter feeding.

Although the animal can filter feed while partially submerged in the sand, this type of feeding is not limited to this position. It can be conducted while the animal is lying on its side on the bottom or even freely swimming since the pleopods continue to function. The animals filter feed even while on their backs stuck to the bottom of a Petri dish with petroleum jelly.

Extensive setation on the mouthparts especially maxilla 2; the small size of food particles found in the digestive tract; the close similarity of the mouthparts to *Haustorius* and, even the animals' environment, all point to primarily a filter-feeding existence; but, just as Dennell (1933) shows in *Haustorius*, the animals may, at times, feed on larger food particles. Stained particles of marine algae > 4000 μ in size were taken into the body but in much smaller pieces

than originally fed. *Amphiporeia* must, therefore, occasionally be capable of tearing apart or cutting into pieces large food masses. The animal was never observed to do this.

Particularly during December, January and February, animals kept in holding tanks at the laboratory, left furrows in the sand up to 20 cm. in length by burrowing underneath. It is believed that they fed extensively off buried and interstitial food during these periods. Experiments conducted using stained food material buried a short distance beneath the substrate surface were largely unsuccessful since stain washed out of the sand. It was determined, however, that the animal is capable of utilizing this food source if only to a limited extent.

ii. Stomach Contents

Detritus which could not be classified as either plant or animal was found in the stomachs of 63.16% of the 38 specimens of *Amphiporeia lawrenciana* dissected and examined microscopically (Appendix 7). This usually consisted of long strings or irregular mats of material often dark in color.

Exuviae or the integument of animals were found in the stomachs of 57.90% of the animals. These were identified as being of the species *Amphiporeia lawrenciana*. Material found usually consisted of an assortment of rami from pleopods and parts of rami, calceoli, various other appendages and parts of the integument. It is likely that the animals ingest the molted integument from their own bodies or from litter on the bottom.

Diatoms were found in the stomachs of 23.68% of the animals. Unicellular algae were found in 15.79%; filamentous algae in 34.21% and multicellular algae in 7.90% of the stomachs examined (Appendix 7).

b) Food Selection

i. Particle-Size Selection

It was found from preliminary experiments that *Amphiporeia lawrenciana* show a certain size-range preference for food offered. Appendix 8a and Figure 17 show that 85.7% of the animals offered food in the size range 125-250 μ in experiments 1, 2 and 3 ingested it. Next highest preference was food in the range 63-125 μ accepted by 69.2% of the animals offered it. Food < 63 μ and in the range 250-500 μ was accepted by 50% of the animals in each case. Food larger than 500 μ was accepted by an increasingly smaller percentage of animals; however, there was a slight increase in the percentage of animals accepting food larger than 4000 μ (Fig. 17).

Appendix 8b shows that 75% of medium length animals (7 - 8.5 mm.) accepted food in the size range 63-125 μ, the only size offered in experiments 4 and 5. Approximately half the small (5 - 6.5 mm.) and large (9 - 10.5 mm.) animals ingested food of this size range. It should be noted that only one out of 10 small animals accepted food of this size in experiment 4 while 8 out of 10 accepted the same food size in experiment 5. Also, 6 out of 10 large animals accepted in experiment 4 while 4 out of 10 accepted in experiment 5 (Appendix 8b).

Although no distinction of sexes was made in the first five experiments, it was noted that the animals without any solid food in

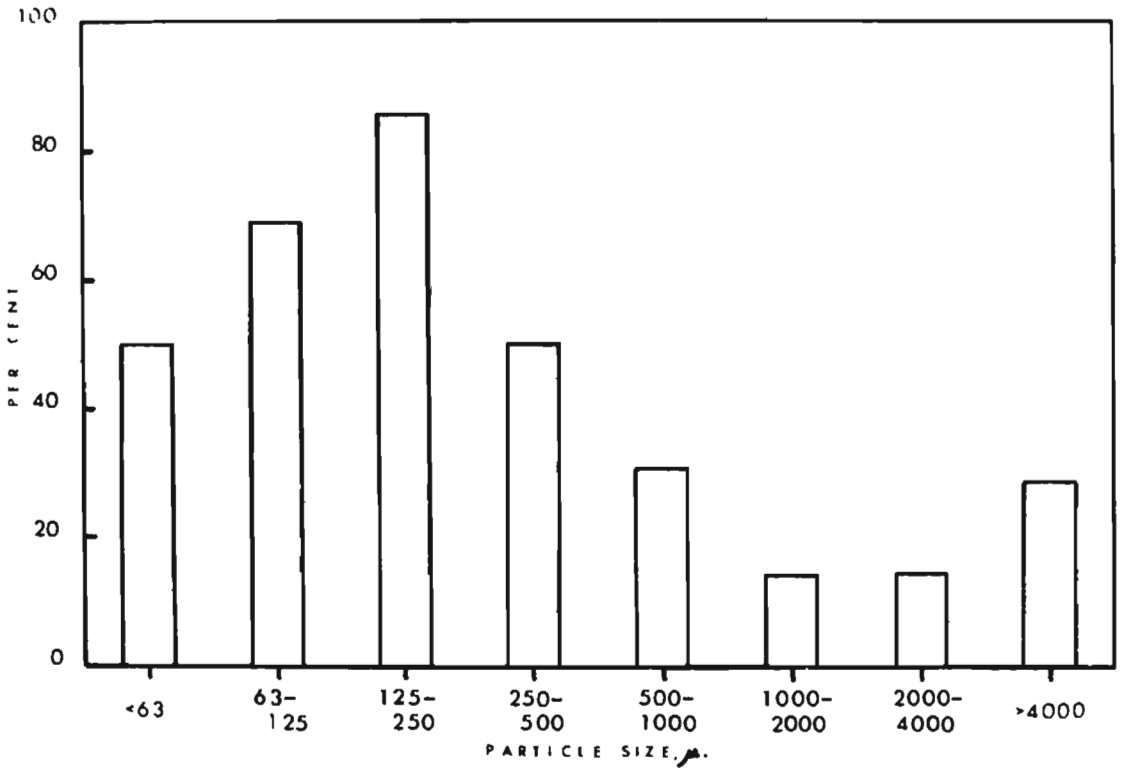


Fig. 17. Percentages of *Amphiporeia lawrenciana* ingesting food material of eight particle-size ranges in three experiments (pooled results).

the digestive tracts were invariably females with long setae on their oostegites and usually ovigerous.

Appendix 8b gives somewhat inconclusive results from experiment 6. In the experiment 40% of the medium length (7 - 8.5 mm.) and 40% of the large (9 - 10.5 mm.) females with embryos in the brood pouches accepted the one food size range, 63-125 μ, offered. For females without embryos but long setae on the oostegites 100% of the small (5 - 6.5mm.) animals accepted the single food size offered but none in any other length class ingested it.

In the seventh and final experiment of the series, 100% of the female animals with hatched young in brood cases ingested the single size range, 250-500 μ, of food offered (Appendix 8d and Fig. 18). Exactly 80% of the females with D-stage embryos and 20% of the females with A-stage embryos in the brood cases ingested the food offered. This is quite significant in that it may indicate a slowdown or complete cessation of feeding while the eggs are enlarging inside the ovaries and for a period after the embryo have been deposited in brood pouches. At that point, however, as the embryos begin to develop, the females may gradually resume feeding until normal feeding is attained around the time when the first young animals appear. Since laboratory studies were not conducted to determine the duration of embryo development, it is not known how long this might be.

Since only 40% of the male animals offered food in the size range 250-500 μ ingested, there may also be a similar slowdown of feeding at certain times of the year. However, it is also possible that this was caused by the inability of these relatively small animals (5-6.5 mm.)

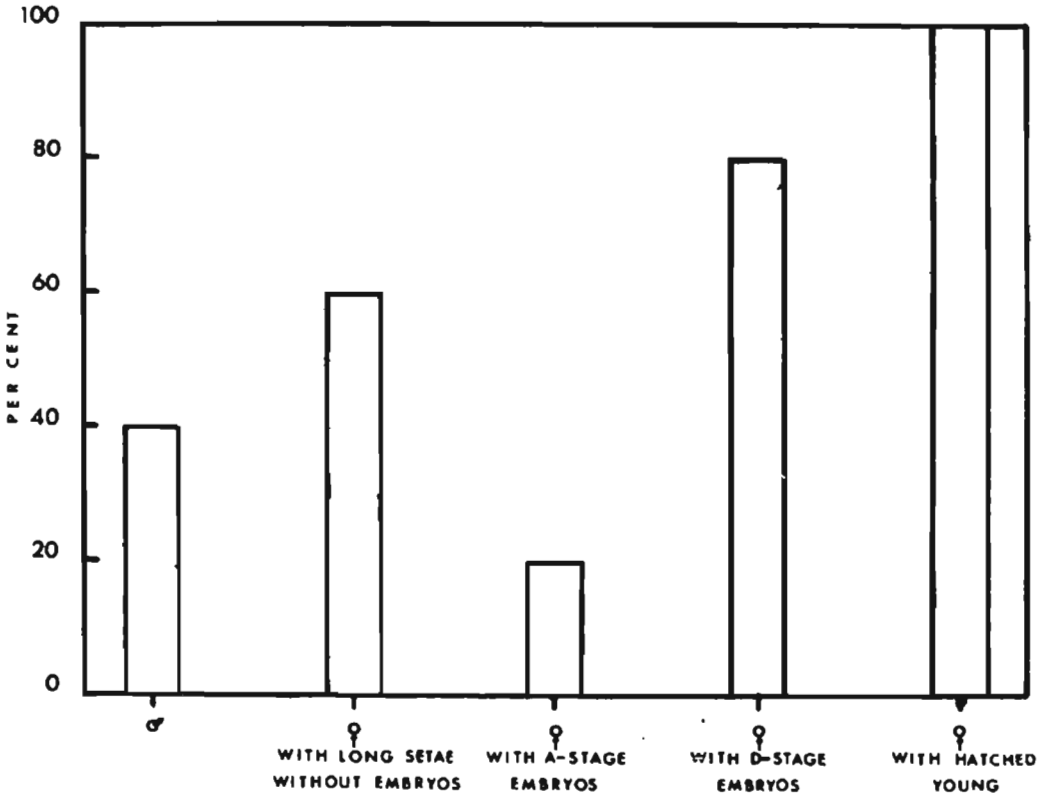


Fig. 18. Percentages of *Amphiporeia lawrenciana*, males and four types of females, ingesting food of the particle-size range 250-500 μ.

to ingest food larger than the optimum size (page 74).

Examination of the mouthparts of both males and females with and without long setae on their oostegites and with embryos at various stages of development did not show any evidence of degeneration of these structures at any time during the life cycle.

ii. Mouthpart Measurements

Maxilla 2, the main filtering structure, consists of two lobes, the inner lobe and external lobe (Fig. 4). The external lobe has two rows of setae. One row consists of thick stout setae while the other has a more slender type. The two sets of measurements from these are very similar and have been combined. The inner lobe has one row of long medial setae and two rows of marginal setae; the latter two rows are very similar to those found on the external lobe and measurements between them have been combined also.

Mean distances between the medial setae and marginal setae of the inner lobe of one 9 mm. female are 11.00 and 8.12 μ respectively (Appendix 9a). The mean for the external lobe setae of this animal is 5.55 μ. Appendix 9b shows that weighted mean distances for the medial and marginal setae of the inner lobe of maxilla 2 of 17 specimens of *A. lawrenciana* is 8.90 μ and 7.91 μ respectively. It is 6.49 μ for the external lobe setae of these animals.

Fig. 19 shows regression lines calculated by the method of least squares for the three sets of setae of maxilla 2 and animal length. Distances between the marginal setae of the inner lobe and the setae of the external lobe show only slight positive correlation

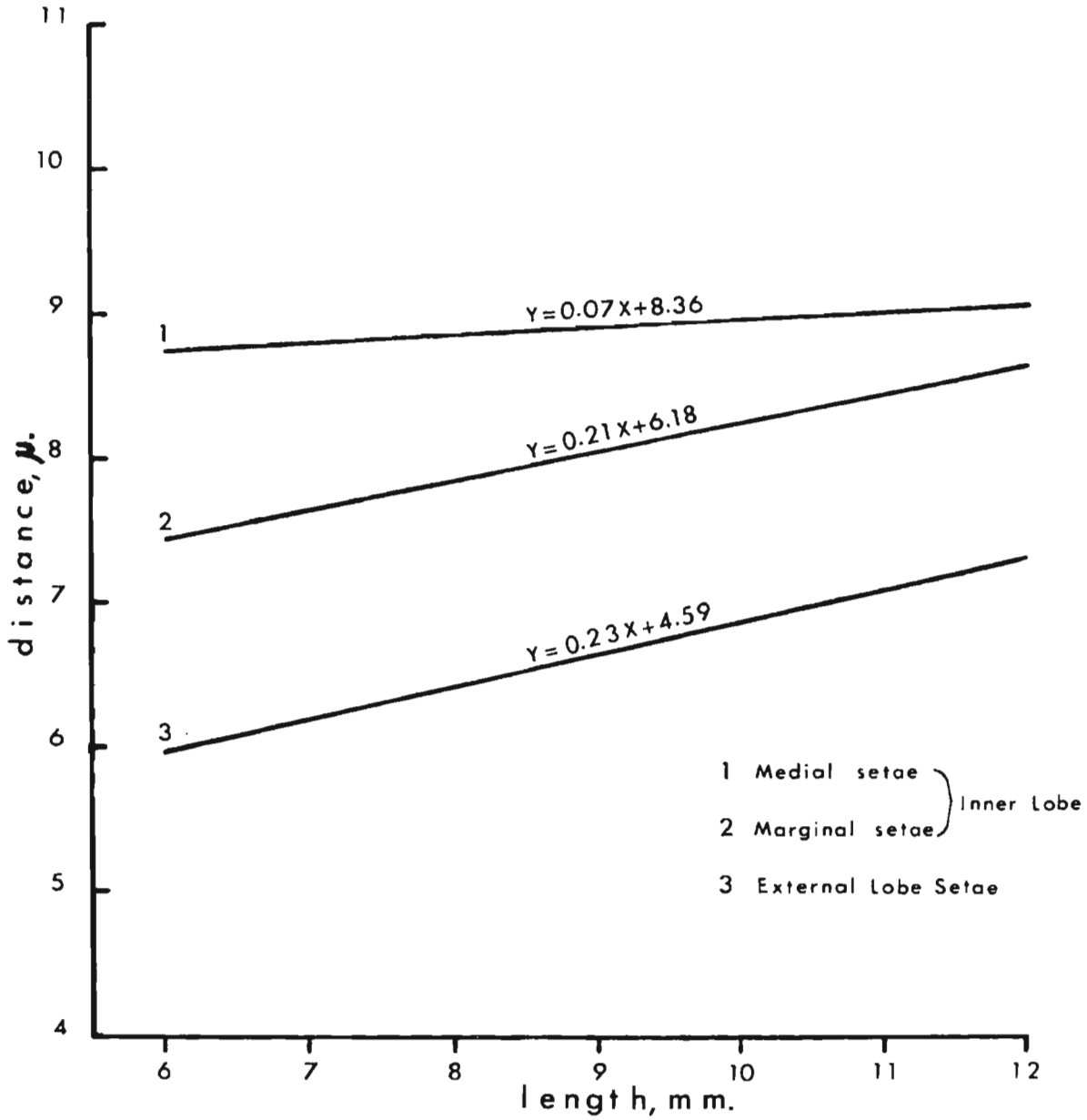


Fig. 19. Mean distance (weighted) between the setae of the inner and external lobes of maxilla 2 per length of animal.

with animal length ($r = 0.54$ and $r = 0.46$ respectively); for the medial setae of the inner lobe there is no correlation of distances with animal length ($r = 0.20$). These results are not surprising in view of the inconclusive results obtained from two experiments conducted to determine any relationship between preferred food particle size and animal length.

Regression line formulas for the medial and marginal setae of the inner lobe of maxilla 2 are $y = 0.07x + 8.36$ and $y = 0.21x + 6.18$ respectively; the formula is $y = 0.23x + 4.59$ for the external lobe setae (where x = distance between the setae and y = animal length).

iii. Food-Type Selection

Positive results were obtained from preliminary experiments conducted to determine if *Amphiporeia lawrenciana* select one food type over another offered. In the first two of these marine algae (*Fucus*) was selected in preference to terrestrial plant material (cabbage) and meat (steak). In a third preliminary experiment a second species of marine algae (*Laminaria*) was substituted for the cabbage and it was found that both *Fucus* and *Laminaria* were selected by about equal numbers of animals and both selected in preference to the steak by all animals.

Gut contents of animals kept in the running seawater system was brown in most animals dissected. Control animals kept also in the system and fed no food except that entering in the running seawater had brown gut contents as well.

In a fourth preliminary experiment small, medium and large animals fed homogenized *Mytilus*, without the shell, rejected the food offered in all cases.

Appendix 10 gives the results of a food type preference experiment. Figure 20 shows that 77.8% of the animals offered *Strongylocentrotus* or sea urchin food stained and homogenized accepted it. None of the animals offered *Mytilus* food ingested it as in the fourth preliminary experiment. Varying percentages of each of the other groups offered animal food, however, ingested it (Appendix 10). Only 44% of the animals offered *Laminaria* food ingested it. This is surprising in view of the high percentages ingesting marine algae food offered in each of the preliminary experiments.

In a control in which nine animals were kept with experimental animals but in a separate container in the seawater system and given no stained food, the brown coloration of normal feeding was observed when they were dissected. A number of other animals from holding trays at the laboratory dissected at this time also showed normal feeding.

3. Substrate Selection

a) Color

Appendix 11a gives the results of six substrate color selection experiments which actually seem to show that *A. lawrenciana* is attracted to "home" substrate or material in which it had originally been living either in the field or at the laboratory.

Results of the first three combined and the latter three combined are shown in Figure 21. The graph shows that more animals selected red

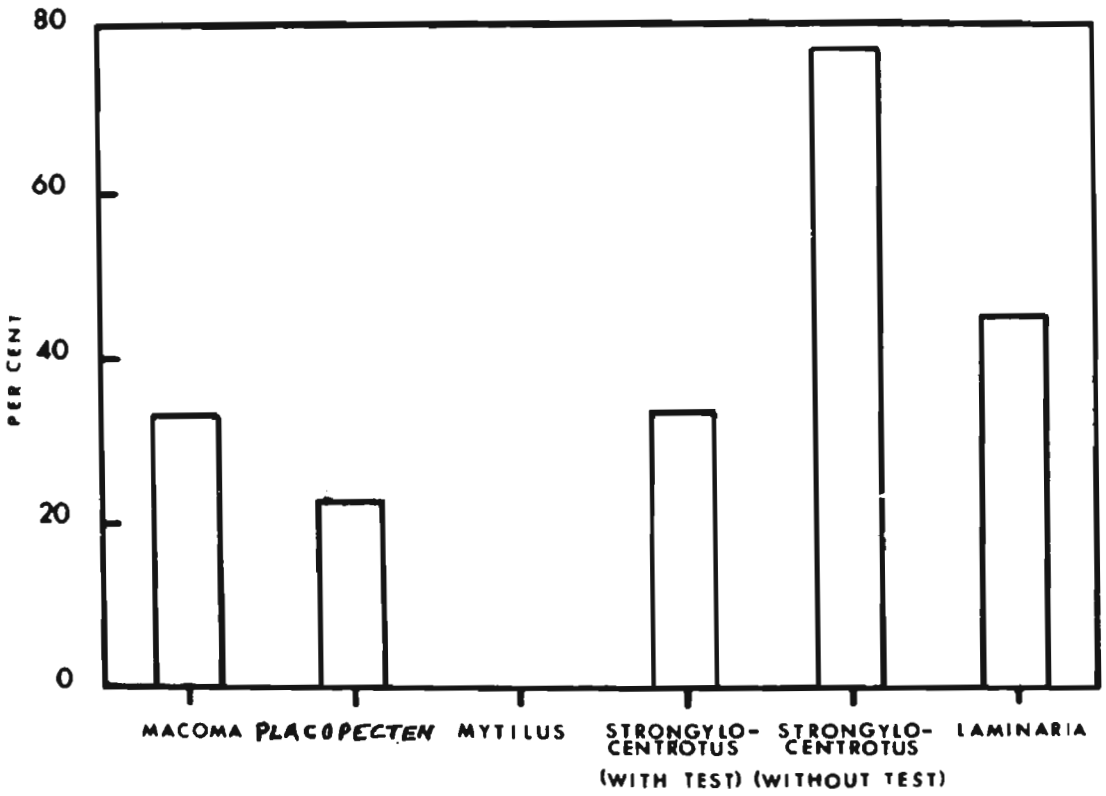


Fig. 20. Percentages of *Amphiporeia lawrenciana* ingesting food (particle-size 125 -- > 4000 μ) of six different types.

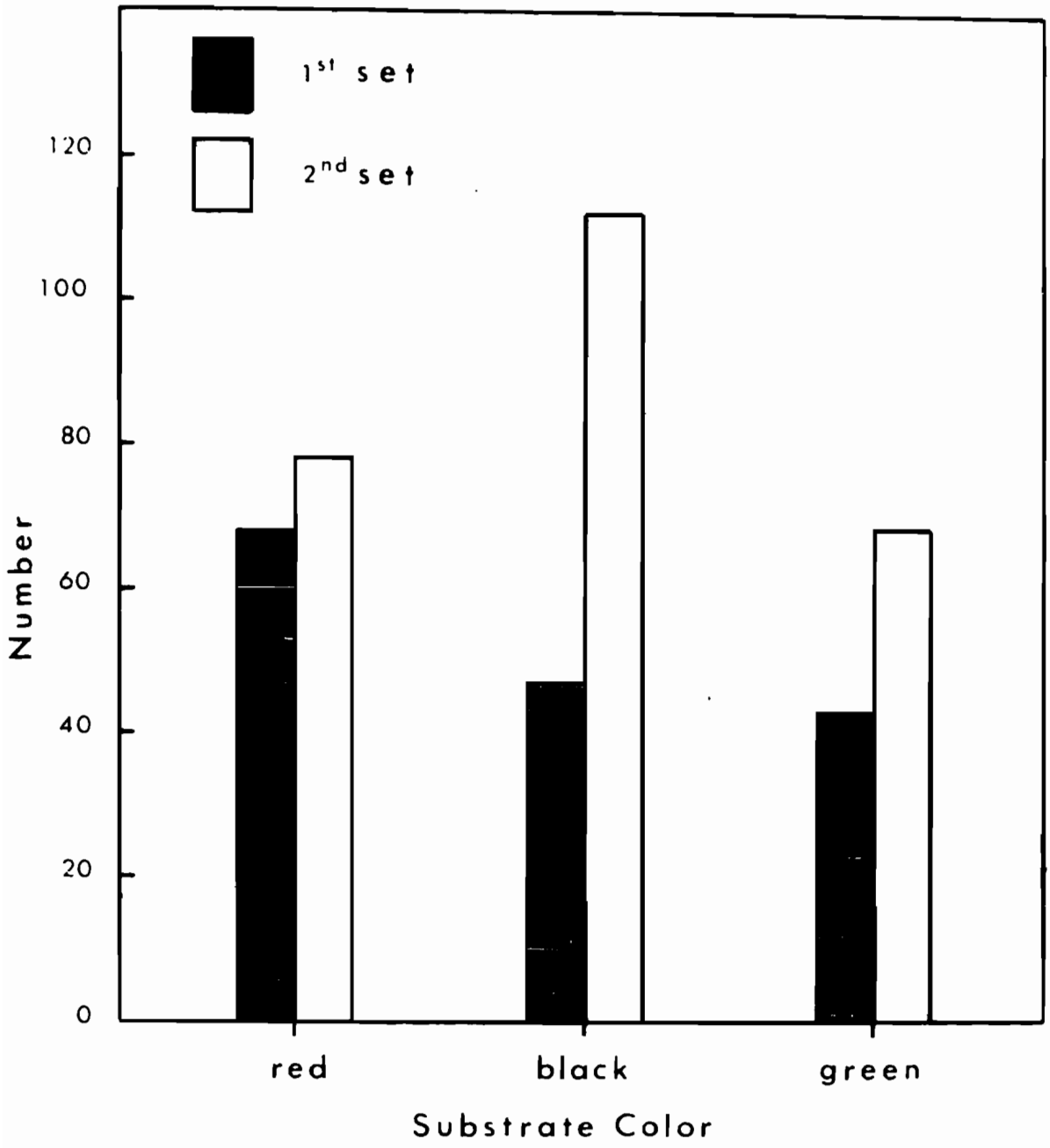


Fig. 21. Relationship of the number of animals making a choice of one of three substrate colors in two sets of experiments (three experiments each).

substrate in the first set and that more animals selected black substrate in the second set. To test the null hypothesis that the animals selected all of the three substrate choices in a random fashion in each of the two sets a chi-square test was applied (Table 14).

Table 14

Chi-square tests applied to two combinations of three experiments each on substrate color selection in *A. lawrenciana*

Total Number Animals Used	Total Selecting Substrate	Actual No. /Container	Expected No. /Container	X^2(d.f.2)	Result
180	158	red - 68	52.67	6.85	< .05
		black - 47	52.67		
		green - 43	52.67		
270	258	red - 78	86	11.78	< .005
		black -111	86		
		green - 68	86		

The probability that there could be a larger value of chi-square was < 0.05 for the first combination and < 0.005 for the second combination; the hypothesis of random selection was rejected in each case. *Amphiporeia lawrenciana* selected red substrate in preference to black or green substrate in the first combination and black in preference to red or green in the second.

Appendix 11b gives the results of five control experiments which are used with both the substrate color selection and the particle-size selection experiments. Figure 22 shows that with the exception of the substrate in containers No. 2 and 3 the material of the same size range and color in the control experiments was accepted by approximately the

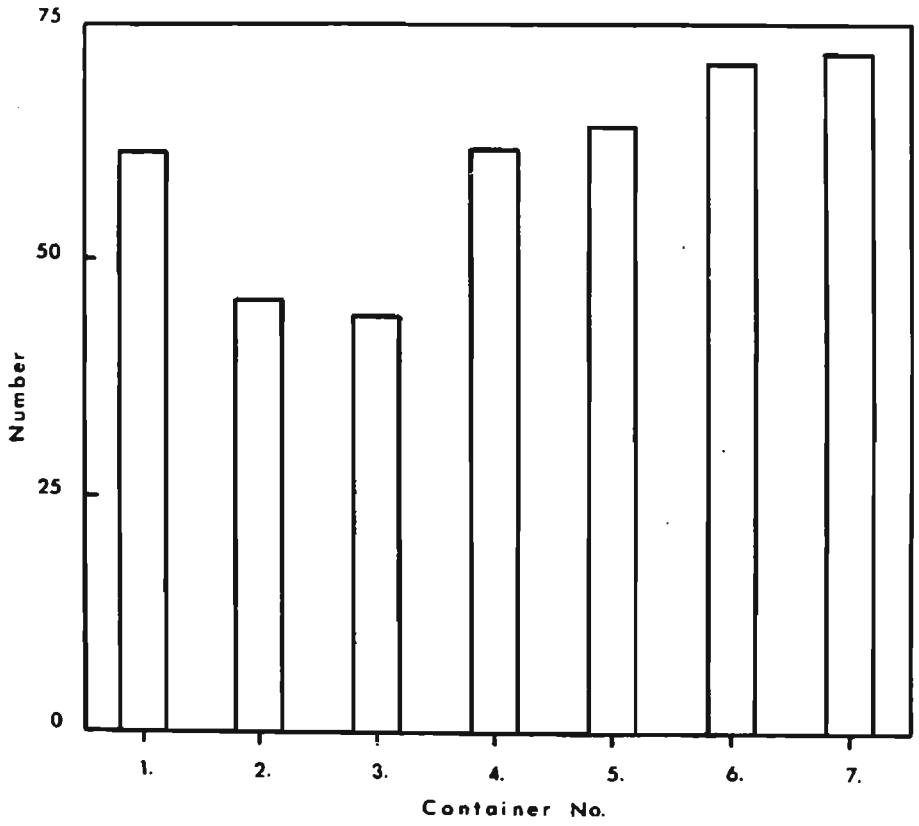


Fig. 22. Relationship of the number of animals making a choice of one of the seven containers in seven control experiments (pooled results). Each was incinerated for 24 hours at 600°C.

same number of animals. To test the null hypothesis that the animals selected any one of the seven substate choices, which were all of the same color, in a random fashion a chi-square was applied (Table 15).

Table 15

Chi-square test applied to a combination of seven control experiments on color selection in *A. lawrenciana*

Total Number Animals Used	Total Selecting Substrate	Actual No. /Container	Expected No. /Container	χ^2(d.f.2)	Result
700	421	62	60.14	12.32	< 0.10
		46	60.14		
		44	60.14		
		62	60.14		
		64	60.14		
		71	60.14		
		72	60.14		

The probability that there could be a larger value of chi-square was < 0.10 for the seven experiments combined; the hypothesis for random selection was accepted. *Amphiporeia lawrenciana* showed no preference for any one of the seven containers of substrate when the color and grain size were the same in each container.

Evidence for color selection is not conclusive since most of the animals used in the second combination came from a black substrate habitat at Salmon Cove and were kept in black substrate from the same location at the laboratory. This could have had a significant effect on the choice of black substrate. Furthermore, some of the animals kept at the laboratory and used in the first combination came originally from red substrate at the bottom of Logy Bay. This could

have had a significant effect on the choice of red substrate. Since the number of animals selecting red substrate in the first combination was only 21-25 more than the number selecting black and green respectively and the chi-square value barely falls inside the critical region, the choice is not highly significant. In both cases, however, it seems that there may be other factors apart from color, when the grain size is similar, which attracts the animals to a particular kind of substrate.

b) Particle Size

Appendix 12a gives the results of five substrate particle-size selection experiments using material incinerated for 24 hours at 600°C. Particle sizes used in each of the seven containers are given in Table 4. Figure 23 shows that the animals selected substrate material within the size range 125-2000 μ (4 containers) in the largest numbers. To test the null hypothesis that the animals selected all of the seven substrate choices randomly a chi-square test was applied (Table 16).

The probability that there could be a larger value of chi-square was < 0.005; the hypothesis of randomness in the selections was rejected. The animals selected substrate in the particle size range 125-2000 μ in preference to material smaller than 125 μ and larger than 2000 μ.

The controls used in this experimental series are the same as those used in the color selection experiments (Fig. 22 and Appendix 11b). Animals selected randomly when the material in each container was incinerated (600° for 24 hours) and all was of the same grain-size range and color (Table 15).

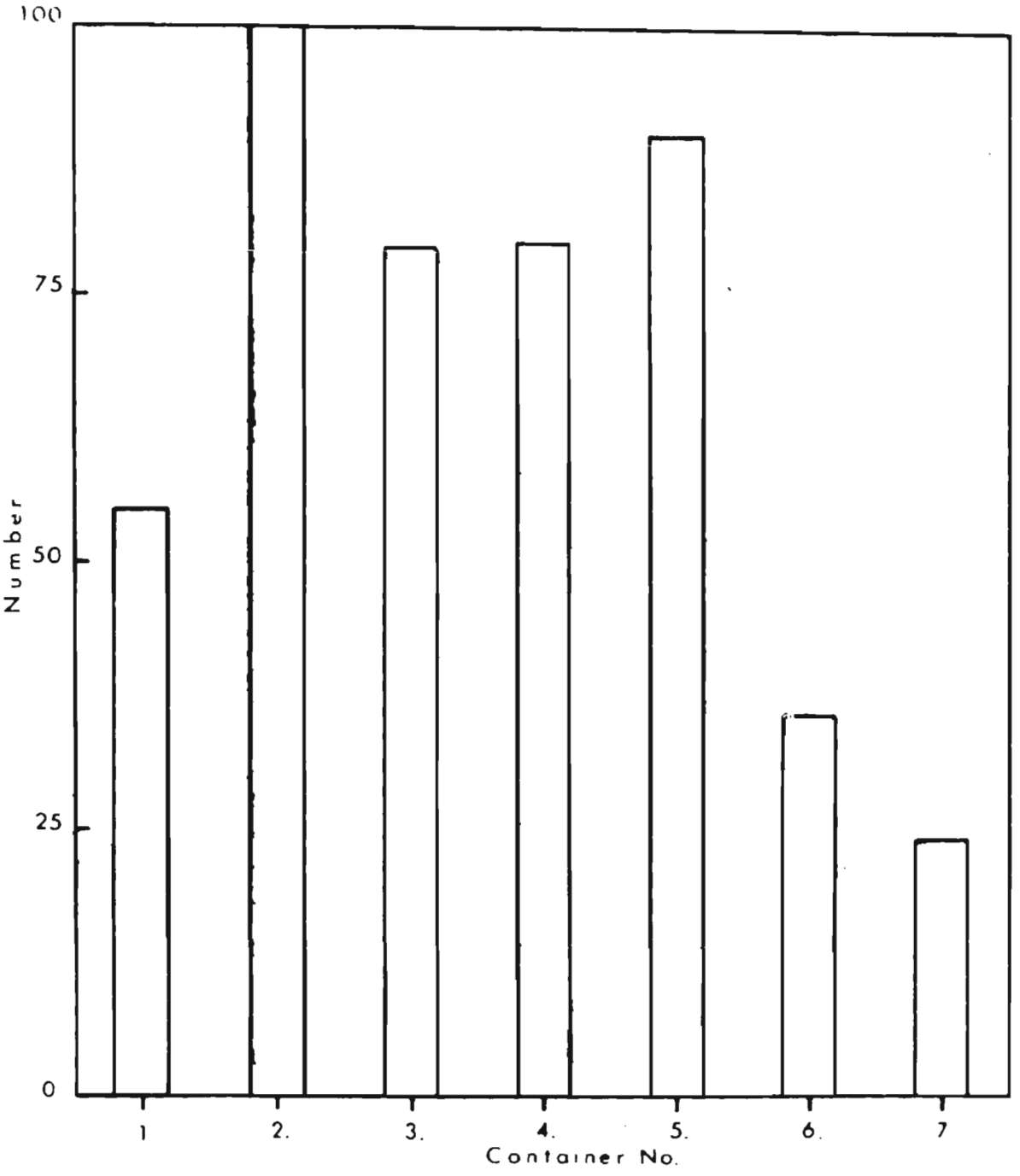


Fig. 23. Relationship of the number of animals making a choice of one of seven substrate particle sizes in five experiments (pooled results).

Table 16

Chi-square test applied to five experiments of the first series on substrate particle-size selection in *A. lawrenciana* (pooled results)

Container Number	Substrate Particle Size, μ	Actual No. /Container	Expected No. /Container	χ^2(d.f.-6)	Result
1	63-125	55	67.43	78.83	< 0.005
2	125-250	100	67.43		
3	250-500	79	67.43		
4	500-1000	80	67.43		
5	1000-2000	98	67.43		
6	2000-4000	36	67.43		
7	> 4000	24	67.43		
	Total	472*	472.01		

*Total number of animals used in the five experiments was 700.

Appendix 12b gives the results of the second experimental series of seven experiments in which substrate of seven specific size ranges; combinations of these size ranges and unsorted material from Salmon Cove were used. Particle sizes used in each substrate choice are given in Table 4. All substrate was dried for 24 hours at 60°C. Excluding unsorted material from Salmon Cove the combined results of these experiments are given in Figure 24 and Figure 25.

Figure 24 shows that the animals selected substrate material within the size 125 - 2000 μ (4 containers) in the largest numbers. To test the null hypothesis that the animals selected all of the seven substrate choices randomly a chi-square test was applied. (Table 17a).

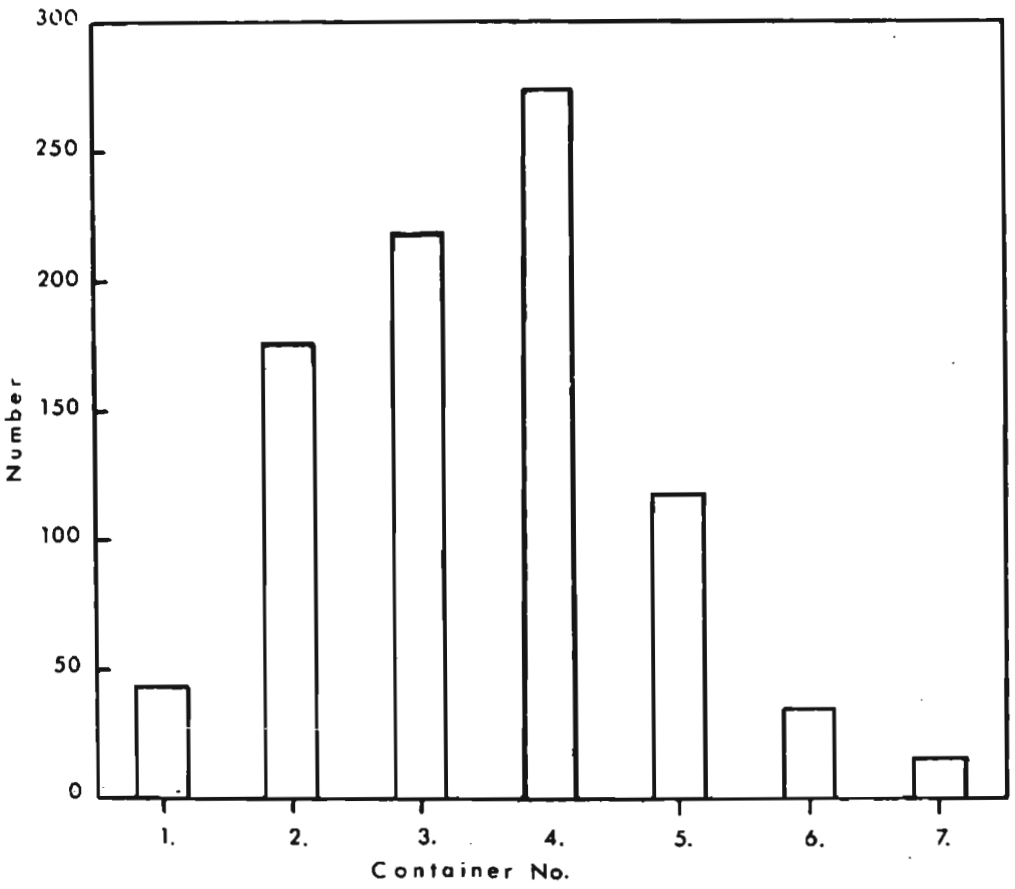


Fig. 24. Relationship of the number of animals making a choice of one of seven substrate particle-sizes in the first part of seven experiments in the second experimental series (pooled results).

Table 17

Chi-square tests applied to the first (A.) and second (B.) parts of the second experimental series on substrate particle-size selection (pooled results of seven experiments) in *A. lawrenciana*

A.

Container Number	Substrate Particle size, μ	Actual No. /Container	Expected No. /Container	χ^2(d.f.-6)	Result
1	63-125	43	125.57	48.27	< 0.005
2	125-250	175	125.57		
3	250-500	218	125.57		
4	500-1000	274	125.57		
5	1000-2000	118	125.57		
6	2000-4000	35	125.57		
7	> 4000	16	125.57		
	Total	879*	879.99		

B.

Container	Substrate Particle Size, μ	Actual No. /Container	Expected No. /Container	χ^2(d.f.-5)	Result
A	1/3(125-250) 2/3(250-500)	208	118.83	26.41	< 0.005
B	2/3(125-250) 1/3(250-500)	172	118.83		
C	1/3(250-500) 2/3(500-1000)	156	118.83		
D	1/3(500-1000) 2/3(1000-2000)	129	118.83		
E	1/3(1000-2000) 2/3(2000-4000)	34	118.83		
F	1/3(2000-4000) 2/3(> 4000)	14	118.83		
	Total	713*	712.98		

*Total number of animals used in the seven experiments was 1960.

Probability that there would be a larger value of chi-sqaure was < 0.005; the hypothesis of randomness was rejected. The animals selected material within the size range 125-2000 μ in preference to material larger or smaller. This part of the experimental series and the results from it are identical to the first experimental series on substrate particle-size selection where seven grain size choices were also used.

Figure 25 shows that the animals selected material of smaller grain size mixtures in the second experimental series. There was a steady decrease in the number of animals selecting as the mixtures offered became larger (Fig. 25). To test the null hypothesis that choice of all mixtures was made randomly, a chi-square test was applied to the second part of the results from this experimental series (Table 17b).

Probability that there could be a larger value of chi-sqaure was < 0.005; the hypothesis of randomness was rejected. Largest numbers of animals selected a mixture of material 1/3 in the grain-size range of 63-125 μ and 2/3 in the range 125-250 μ (Table 4). Least number of animals selected a mixture of material 1/3 in the grain-size range of 2000-4000 μ and 2/3 in the size range > 4000 μ.

Finally, Appendix 12c gives the results of five control experiments run in conjunction with the second series on particle-size substrate selection experiments. Figure 26 shows that there was an erratic pattern of selection in the control experiments. To test the null hypothesis that the animals selected any one of the seven substrate choices (all of the same grain-size range) randomly a chi-square test was applied (Table 18).

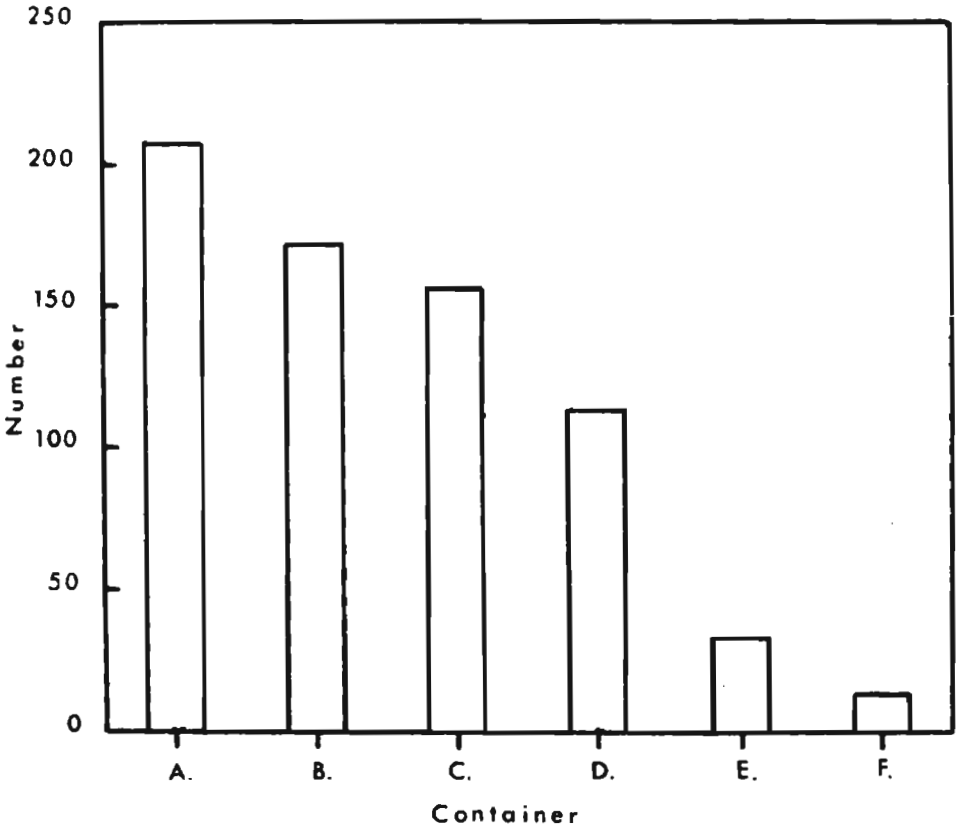


Fig. 25. Relationship of the number of animals making a choice of one of six substrate particle-size mixtures in the second part of the second experimental series (pooled results).

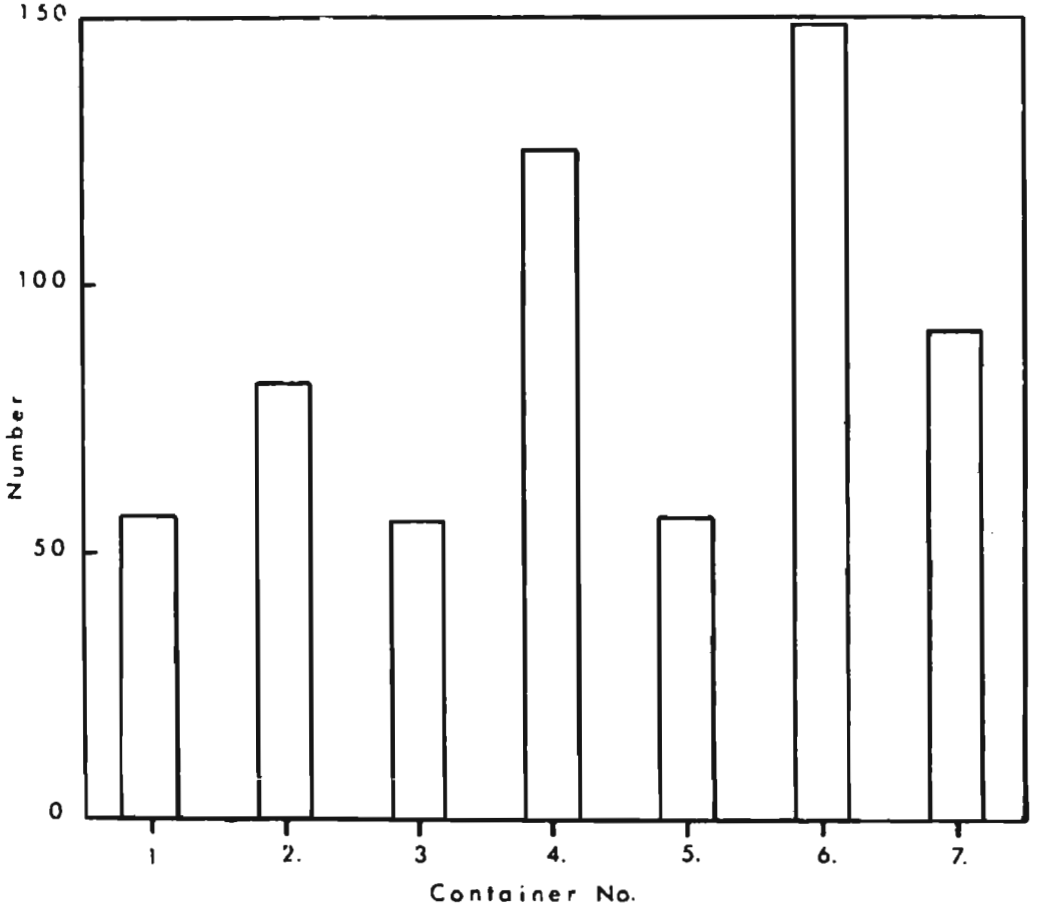


Fig. 26. Relationship of the number of animals making a choice of one of the seven containers in five control experiments (pooled results). Each container had substrate of the same particle-size range and color dried (60°C.) overnight.

Table 18

Chi-square test applied to the control experiments of the second series on substrate particle-size selection (pooled results of five experiments) in *A. lawrenciana*

Container Number	Substrate Particle Size, μ	Actual No. /Container	Expected No. / Container	χ^2(d.f.-6)	Results
1	Unsorted	57	88	92.55	< .005
2	"	82	88		
3	"	56	88		
4	"	125	88		
5	"	56	88		
6	"	149	88		
7	"	91	88		
	Total	616*	616		

*Total number of animals used in the five experiments was 700.

The probability that there could be a larger value of chi-square was < 0.005; the hypothesis of random selection was rejected in the control experiments. Looking more closely at this unusual result for the control series, it is evident from Fig. 25 that certain containers of dried material (60° for 24 hours) were preferred to others offered. Although the color and grain-size range remained the same in all of these, since the substrate was dried only, some of the organic material may have still remained and become distributed unevenly in the control containers and acted as attractants in this way. This is the only explanation which can be offered assuming all other factors remained constant.

The unsorted material from Salmon Cove (Appendix 12b) was selected by the largest number of animals in two of the experiments of

the second series and was high on the list in several of the others. This is not unusual since the animals were taken from this type of habitat and kept in this grain-size at the laboratory.

Varying numbers of animals were found outside all substrate containers in both the experiments and controls (Appendix 12a, 12b, and 12c). Since no pattern is evident in the numbers, it was probably caused by accident.

In all of the grain-size experiments the animals choose substrate within a well defined size range and this size range closely approximates that for the substrate found at Salmon Cove and at beaches throughout Newfoundland where *Amphiporeia lawrenciana* are abundant.

V DISCUSSION

A. Relationship of Distribution and Abundance to Physical and Chemical Factors

Amphiporeia lawrenciana (Shoemaker 1929) was found in Newfoundland at only 28% of all the beaches sampled. Certainly a more exhaustive survey is necessary to say with certainty which factor or factors limit the distribution of the species in Newfoundland waters; however, there are some good indications as to which at least are most important.

The importance of physical as well as chemical factors in the control of bottom-dwelling organisms has recieved a considerable amount of attention from various workers. Bruce (1928) states that in no other region of the biosphere does it appear that purely physical factors of the environment exercise so profound an influence upon living forms as on the seashore. Kindle (1916) concludes that the physical characteristics of the bottom are more effective than great differences in latitude in determining the composition of a fauna. In discussing the sandy beaches of freshwater lakes Pennak (1940) states that in contrast to ordinary aquatic conditions the psamolittoral organisms inhabit very unstable and unique surroundings largely on account of the effects of factors outside the sand. The amount of capillary water may change; the temperature range may be comparatively great; dissolved oxygen and carbon dioxide may fluctuate and the amount of food material in the sand may be inconstant (Pennak *op. cit.*). In spite of the widespread consensus of opinion on the importance of physical and chemical factors in the environment on the abundance and distribution of organisms, there is some disagreement as to which are most important.

Salinity and temperature are not considered to be limiting factors in the distribution of *A. lawrenciana* in Newfoundland waters. The means and ranges for both these parameters at beaches where the species was found are very similar to the values for beaches where the species was absent. It was found living in substrate as warm as 21°C at Indian Islands in July as well as in sub-zero temperatures at Salmon Cove in February. Tolerance experiments conducted by the author have shown that the animals can survive in temperatures as high as 12.9°C or at room temperature in still water for prolonged periods during January and February when the ambient seawater temperature is -1.0 -- 1.0°C. They were found living in salinities as high as 29.5 ppt. On one occasion the animals were taken from an area where the surface salinity was 6.2 ppt. Even at a depth of 0.5 m. on the bottom where the animals were living, the salinity must have been relatively low.

Suspended matter in the seawater is also not considered to be a major limiting factor to the distribution of *A. lawrenciana*. The mean at beaches where the animal was found was only 5.3 mg./l. less than at beaches elsewhere in Newfoundland. Jansson (1969b) considers also that food or organic material present in the environment is not an important limiting factor for fauna of marine sandy beaches since it is not likely to be low enough to be important. An accurate means of analysis and the lack of time prevented a comparison of the organic content of the substrate at beaches sampled in this study but the same probably holds true for this parameter as well.

Oxygen content of the water and substrate were not recorded in this study but its importance cannot be ignored. Jansson (*op. cit.*)

states that little is known of the response to controlled oxygen conditions but that field distributions of several species have been interpreted as a response to oxygen conditions.

Two factors which have been studied and are considered important in the distribution of *A. lawrenciana* in Newfoundland are particle-size of the substrate and exposure of the beach.

Considering the former it was found that at beaches where more than 83% of the substrate is within the 125-1000 μ range *A. lawrenciana* were collected in abundance. At Salmon Cove, where there is also a good population of this species, 95.27% of the substrate is within this size range. Some exceptions have been found. At two beaches 55.34% and 48.93% of the substrate respectively is within the 125-1000 μ size range, yet the animal was found there, admittedly in relatively small numbers. Furthermore, two beaches had more than 84% and eight beaches had more than 60% of the substrate within this size range, yet the animal was not found at any of them.

Exposure seems to be an important factor to consider in these cases. At five of the eight beaches with more than 60% of the substrate within the considered optimum particle-size range, and where *A. lawrenciana* was absent, good protection was afforded either by offshore islands or where the beaches were located inside bays or barachois. Cape Ray (outside the barachois), one of the remaining three beaches where the species was absent, had 75.18% of the substrate within the considered optimum size range. Since it is known that the animal does occur there (D. H. Steele, pers. comm.), less than ideal sampling conditions at the time, including very heavy surf action, is thought to have prevented collection. At the

other two beaches, exposure and the substrate particle-size seem to be suitable yet the animal was not found. All of the beaches where the species was collected, including those with less than 56% of the substrate within the considered optimum size range, were well exposed to the open ocean and heavy surf action.

Conclusions from field studies have been confirmed by several laboratory experiments on substrate selection. These have shown that *A. lawrenciana* significantly select substrate within a particular size range preferring material within the range 125-2000 μ. Very few animals selected substrate smaller than 125 μ and larger than 2000 μ. Furthermore, experiments which were designed to determine if the species has a color preference of substrate actually seem to show a preference for "home" substrate, i.e., substrate from which the specimens used were originally collected or in which they were kept at the laboratory for some time.

Several workers indicate the importance of particle-size in the abundance and distribution of sandy beach organisms. Jones (1970) found that sand particle-size is of primary importance in determining the relative geographical distribution of the isopods *Eurydice pulchra* and *E. affinis* in areas of Britain where they occur together. He also indicates that large populations of *Eurydice* may be related to wave action received by the beach. In a field experiment conducted in North Wales, Boden (1962) found that large numbers of Nematoda were found in the finest grades of sand. The archiannelid *Protodrilus adhaerens* did not occur in substrate with grain sizes 500 μ in diameter; *Protodrilus chaetifer* was commonest in the 210-150 μ sample. Mills (1967) notes

that the amphipod *Ampelisca vadorum* found in Long Island Sound prefers sediment where the major proportion falls in the 1.0 - 2.0 mm. (1000 - 2000 μ) range whereas the amphipod *A. abdita* prefers sediment where the major proportion falls in the 0.10 - 0.5 mm. (100 - 500 μ) range.

Croker (1967a) notes that *Neohaustorius schmitzi* and *Haustorius* sp. preferred cleaner sand over more silty and debris-laden sand in laboratory experiments and that there was a parallel in the field. *A. lawrenciana*, a closely related species, in these studies rejected the finer, silt-laden substrate in selection experiments and were found in clean, wave-washed sand at all areas of occurance in the field. Holme (1949) found that *Bathyporeia pilosa; Eurydice pulchra; Corphium arenarium* and *Hydrobia ulvae* prefer clean, loose sand since they were absent from muddy sand in the Exe Estuary in Great Britain. Meadows (1964) shows that at least one species of amphipod *Corphium vulutator* preferred mud both in the laboratory and in the field. *C. arenarium*, however, choose sand both in the laboratory and in the field.

Weiser (1959) considers it unquestionable that texture of the substrate exerts an influence on the fauna. He discusses the 200 - μ line as a "critical grain size" constituting the approximate lower limit of distribution for such animals as *Protodrilus flabelliger; Neveilla antennata; Enoploides harpax* and *Onyx ragata* and the upper limit of distribution for *Sabatiera sp.; Theristus wimmer; Pareurystomina pugetensis* and *Odontophora peritricha*. He believes that it is around this grain size that interstitial spaces which exist in coarser sand are beginning to fill up with fine material. The 200 - μ line would, then, separate species that live in interstitial spaces from those

that burrow through the substrate. Since 125-250 μ is the lowest preferred range of substrate for *A. lawrenciana*, it is possible that the postulated 200 - μ line of division has some merit. The species is an accomplished burrower.

The fact that more *A. lawrenciana* selected unsorted substrate from Salmon Cove, dried at 60°C for 20 hours, in the first experiment of the second series on particle-size substrate selection than any other type of substrate offered is a good indication of the attractive factor of sand from the natural habitat. In the six subsequent experiments there was a progressive decrease in the number of animals selecting unsorted substrate thus showing that this attractive factor decreases with time and prolonged submersion in seawater outside the natural habitat. Apparently, the attractiveness is maintained even after drying at 60°C. Preliminary experiments of this type repeatedly showed this phenominum.

The color selection experiments confirm that qualitative ' differences between sands, apart from grain size, play an important role in the selection of substrate by *A. lawrenciana* since it was found that the animal apparently prefers "home" or natural habitat substrate to others offered. Gray's (1966b and c) conclusions on the interstitial arachiannelid *Protodrilus symbioticus* Giard are similar to these findings.

He found that this animal responds thigmotactically to the natural substrate and to an artificial one of glass beads (1966b) but, in a later paper (1966c), concludes that differences in the attractiveness of certain sands of the same grain size is due to the presence of certain

species of bacteria and is mediated through the films they form on sand grains. The attractive factor of natural sand to *P. symbioticus* is due to the surface film on the sand grain surface of certain favorable species of bacteria. Meadows (1964) and Meadows and Anderson (1966) working with the amphipods *Corphium* species and micro-organisms on sand grains in marine and freshwater environments reach a similar conclusion concerning the attractive factor of certain sands.

Since *A. lawrenciana* did not immediately make a choice of one particular type of substrate in the color selection experiments but swam from one container to the other and around the holding tank before selecting, the response may be more thigmotactic having something to do with the physical nature of the grains rather than a chemotactic response to a bacteria film around the sand grains. In the two sets of control experiments used with the substrate selection experiment one utilized unsorted material dried at 60°C. while the other utilized unsorted material incinerated at 600°C., and both came from the Salmon Cove area, yet there was no apparent difference in the numbers of animals found swimming outside the containers in the holding tanks for the two sets. This seems to indicate that the incinerated material was no more unattractive than the dried material. It could be of course that the bacteria film was destroyed in both cases and that this attractive factor was absent. Since no additional experiments of this nature were conducted, further study is necessary to draw any firm conclusions.

The only information obtained on local distribution on the beach at Salmon Cove of *A. lawrenciana* is that there is probably a band of concentration of the animals during the last week in May 25 m. from LWS at about the level of the temporary stations. Laboratory observations and measurements have shown that the animals can burrow to a maximum depth of 15 mm. The lower limit of this vertical gradient is utilized by only the larger animals since there is a straight line relationship between the length of the animal and the depth burrowed.

Jansson (1962, 1966, 1967a, 1967b, 1967c, 1967d, 1967e, 1968a) in a series of papers culminating in a summary of most of his previous publications (Jansson 1968b) states that most studies of the localization of animals in the gradient network, combined with laboratory studies, have been concerned with non-tidal beaches. Distribution of most species is to a great extent explained by their reactions to well-defined horizontal and vertical temperature and salinity gradients. Grain size proper of the substrate he considers not to be significant as an environmental factor except in the light of incorporated factors such as water content; circulation of interstitial water and oxygen availability. Tolerance puts the outer limits to interstitial animals in the field while preferances are responsible for the narrow localization within the tolerance zone (Jansson *op. cit.*).

It is unlikely that most of the physical and chemical parameters recorded at Salmon Cove throughout the year come even close to the tolerance level. Wide variations have been noted in some of these but the species was present throughout the year. Biological factors of the population resulted in the rapid increases in abundance throughout the

summer and fall; the death of large numbers of the older population can account for some of the rapid decrease in population abundance beginning in December. These factors, however, are not believed to be entirely responsible for the extreme decrease in abundance in the winter months particularly in January when the number of animals taken in the quantitative samples was 12/0.5 $m.^2$ as compared with 1922/0.5 $m.^2$ in October.

Although the substrate organic content at Salmon Cove was low during the winter months, there were periods during early summer and fall when lower values were recorded. Similarly, although salinity of the seawater reached its lowest point in February, there were extreme fluctuations in this parameter up to early spring. The two factors which remained consistently low during the winter months and could, therefore, have had some effect on population abundance were suspended matter in the seawater and temperature of the seawater and substrate. Some animals remained in the area during January and February, when the lowest temperatures were recorded, but it is unlikely that they could withstand temperatures much lower than -1.0°C. For this reason it is believed that the tolerance limit for low temperature of the species was approached during the winter and they may have responded by either moving outward from the shoreline or burrowing deeply into the substrate. Since no investigations were made to determine this, we can only speculate as to what might have happened to cause the decrease in numbers at the level of the temporary stations during this period.

Colman and Segrove (1955) say that there is a certain amount of rather vague evidence in the literature about the possibility of

seasonal changes in the distribution of faunas in sand. They cite *Haustorius arenarius* at Stoupe Beck, Robin Hood's Bay, Yorkshire, as a possible example of this seasonal change. Its largest numbers were found farther down the shore in April, 1950, than in the previous July. They consider the evidence inadequate but the possibility of a seasonal factor should not be ignored. Likewise, at Salmon Cove the evidence is inadequate and more study is needed to assess the full implication of seasonal variation if there is one. Sameoto (1969a) found that three species of subtidal sand-burrowing haustoriid amphipods at Cape Cod, Massachusetts, migrate into sands just below the low tide zone in May, remain there until late August and then migrate into deeper waters. It is thought that this is a response to changing water temperature (Sameoto 1969b).

It should be noted in conclusion that Bousfield (1970) considers the most primitive or basic members of the haustoriid phylogenetic series (Pontoporeiinae which includes *A. lawrenciana*)occuring along circum-polar sub-arctic shores, including the northern part of the Atlantic coastline, may be in the process of replacement by more recently evolved members of the subfamily Haustoriinae because they are more specialized and more highly adapted to the unstable sandy beach environment. Although *A. lawrenciana* did not occur at all sandy beaches visited, this was certainly not a result of displacement by another more suitably adapted species such as *Haustorius* since no other haustoriids were identified. It was the result primarily of a grain-size preferance. At areas where the species did occur and optimum conditions seemed to exist the highest concentration was 319 animals per $0.1 m.^2$. In this

particular area (Windmill Bight) a similar or possibly higher concentration is known to occur along more than a mile stretch of beach. A possible decrease or complete disappearance of the species is, therefore, certainly not indicated with figures of this magnitude. In fact it seems to be surviving quite well in Newfoundland waters.

B. Reproduction and Life Cycle

Observations confirm that the typical "clasping" or precopula reflex described in more "primitive" gammarian amphipods since the turn of the century and before has been lost in *Amphiporeia lawrenciana*. Holmes (1903); Kinne (1954a); Hynes (1955) and Waterman (1961) discuss the act of carrying by the males of the much larger females in these amphipods; in *Amphiporeia* the act would be physically impossible since the males are considerably smaller than females of the species. The act of copulation itself, however, which is believed to have been observed in this species on four separate occasions, is very similar to that described by Kinne (1954a) for *Gammarus duebeni*. Bousfield (1970) states in his papers that free swarming and pelagic mating has not been observed in this group. Although the mating activity observations made on *Amphiporeia* were somewhat limited and relatively brief in duration, it was found that it can occur in daylight on the surface of the substrate. No evidence of swarming was observed at any time.

Some female *A. lawrenciana* became ovigerous at length 6 mm.; 3 - 18 embryos are produced by females in the length range 6 - 13 mm. This compares with a range of 5 - 25 and a mean of 11.1 ± 4.9 embryos per female for *Haustorius canadensis* and a range of 3 - 18 and a mean of

7.0 ± 2.8 embryos per female for *Neohaustorius biarticulatus* at Cape Cod (Sameoto 1969a). Mean size of the eggs for the latter two species was not given so that a valid comparison between these and *A. lawrenciana* is not possible.

Mean size range from A-stage embryos to hatched young for *A. lawrenciana* was 0.829 - 1.389 mm. for preserved specimens. Living embryos from A-stage to hatched young for *Gammarus setosus* in Newfoundland was 0.600 - 2.330 mm. (Steele and Steele 1970a). Living A-stage embryos were slightly smaller than those preserved in 5% formalin. Living *Gammarus obtusatus* embryos also taken in Newfoundland were of length range 0.576 - 1.850 mm. (Steele and Steele 1970b). A significantly smaller size for preserved specimens was also noted in this study.

A. lawrenciana oogonia begin to enlarge in October and November; the first embryos are deposited in brood pouches in significant numbers in March and the first young appear in brood pouches in late May. This is very similar to *Gammarus obtusatus* (Steele and Steele *op. cit.*) except that it is not known if female *A. lawrenciana* enter a resting stage in September. In *Haustorius canadensis* and *Neohaustorius biarticulatus* the first ovigerous females appeared in late May and the first young in late June for incubation periods of 28 days and 28-35 days respectively (Sameoto 1969a). Although no laboratory studies were carried out, from examination of the samples it is believed that the incubation period for the first brood of *A. lawrenciana* is around 60-90 days at ambient temperatures (range of -1.0 -- 15.0°C, mean of 4.78°C for the year).

A second brood of *A. lawrenciana* is produced from June to September. It is thought that the incubation period for this one is

around 30-60 days.

Only one brood is produced by *Haustorius canadensis; Neohaustorius biarticulatus; Acanthohaustorius millsi* and probably only one for *Protohaustorius deichmannae* (Sameoto 1969a and b). *G. obtusatus* produces three to four broods in Newfoundland; a population in the Bay of Fundy has a similar cycle (Steele and Steele 1970b). *G. setosus* in Newfoundland produces only one brood per year (Steel and Steele *op. cit.*).

Watkin (1939) has found that *Bathyporeia pilosa*, the embryos of which are released in just 15 days, may produce broods all during the year in Kames Bay, Scotland, but that *Bathyporeia pelagica* in the same area is confined to spring and summer breeding periods. The winter breeding cycle for *Pontoporeia affinis* extends from December to May in Wisconsin lakes (Juday and Birge 1927). Segestråle (1967, 1969, 1970 1971a and 1971b) working on the same species, which is a boreo-arctic marine amphipod found also in freshwater lakes, concludes that although it normally breeds during the winter season, it has been found to breed in the summer at depths below 100 m., and *Pontoporeia femorata* also breeds in the summer even at 60 m. Green (1968) in studies of *Pontoporeia affinis* in Coyuga Lake, New York, agrees with these findings.

In *A. lawrenciana* the overwintering generation of females enters the most intense reproductive phase between April and August. During July and August most ovigerous females have released their young and then loose the reproductive characteristic of long setae on the oostegites.

Young or unsexable animals increase in numbers from June to October when the peak is reached. Growth of the young is apparent from samples between August and October, but by November many have

differentiated sexually and have been absorbed into the lower length classes of the adult population. None is present in December.

The samples indicate that the die-off of the older generation begins as early as June and July since there is a decrease in the numbers present in the upper length classes in these months. It is unlikely that many animals survive later than December. The life cycle of most animals is, then, around 12 months.

Sameota (1969a and 1969b) also gives a 12 month life cycle for *Haustorius canadensis; Neohaustorius biarticulatus; Protohaustorius deichmannae* and *Parahaustorius langimerus* as do Steele and Steele (1970b) for *Gammarus obtusatus*. *Gammarus setosus* found in Newfoundland, Bay of Fundy and the arctic may live longer than 12 months (Steele and Steele 1970a).

The overall sex ratio for the year for *A. lawrenciana* was 7 female: 3 male but there was some variation throughout the year particularly during the reproductive period. For *Haustorius canadensis* it was 1:1 at the beginning of the breeding season, fluctuated and then restored to 1:1; for *Neohaustorius biarticulatus* it was 3 female: 2 male at the beginning of breeding, 1:1 in late summer and 3 female: 2 male again in October (Sameoto 1969a). It was 1:1 for *Gammarus obtusatus* throughout the year (Steele and Steele 1970b).

C. Swimming, Burrowing and Feeding

Bousfield (1970) describes species of the genus *Amphiporeia* as "more specialized, obligate sand-burrowing" members of the subfamily Pontoporeiinae. It is certainly true that *A. lawrenciana* is an obligate

sand-burrower since it was not found at any other beach habitat in Newfoundland and even at sandy beaches where it did occur its sand particle-size preference was somewhat narrow (125 - 1000 μ range). This species is characterized by a truncated broad-fusiform body; Bousfield (*op. cit.*) indicates that this may serve the animal by enabling it to burrow more deeply into the substratum and thereby utilize more interstitial food than species of the slender-fusiform body type. He comments that the broad-fusiform body form in effect creates a vertical cylinder in which a hydraulic-tunnelling current can be created by powerfully modified pleopods and the strong current increases the food filtering rate in the water (sand) column. Observations by the author confirm that *A. lawrenciana* is an efficient burrower burrowing relatively deeply into the substrate (maximum of 15 mm. for a 10 mm. animal) and that it probably utilizes some interstitial and buried food material primarily as a filter-feeder but occasionally "raptorially". Powerful and distinct swimming and feeding currents are created in the manner described. It is not considered to be a good swimmer. In almost all aspects, therefore, it fits well the description given for this amphipod group.

As in the case of *Haustorius* (Dennell 1933) *A. lawrenciana* produces swimming currents by means of three sets of modified pleopods. The former, however, swims on its back while the latter swims in a slightly upright position inclined at approximately 35 degrees to the horizontal.

The metachronial beat or out-of-phase motion of the pleopod pairs in both species provides a continuous water current rather than a series of spurts. In spite of this, *A. lawrenciana* flexes and

extends its body while swimming apparently to help increase its speed through the water. The effect is clumsy and awkward movement.

The water vortices created by *A. lawrenciana* which turn and curl up towards the ventral surface provides a very effective aeration system for embryos and hatched young inside the brood pouches of females.

Burrowing for *A. lawrenciana* is also like that described for *Haustorius* by Dennell (1933) but it is probably more efficient in the former since the extended vortices of water moving outward from the sides propel sand in these directions as well as to the rear. *Amphiporeia* is unable to burrow in dry sand as is the case for *Haustorius* (Croker 1967a).

The vigor of burrowing is similar to that described by Croker (*op. cit.*) for the haustoriid species *Neohaustorius schmitzi, Parahaustorius longimerous, Haustorius* sp. (undescribed and closely related to *H. canadensis*), *Acanthohaustorius* sp. (undescribed and closely related to *A. millsi*) and *Lepidactylus dysticus*. The quick withdrawal response when *A. lawrenciana* is touched while burrowing is also similar to his description for these species.

Sameoto (1969a) describes *Neohaustorius biarticulatus* and *Haustorius canadensis* as burrowing upright into the sand using mainly the gnathopods to dig, with the first and second peraeopods and water currents created by the pleopods. His descriptions are similar to that by Watkin (1939) for *Bathyporeia*. Mechanical action of the appendages rather than the force of powerful water currents is thought to be the major means of burrowing in these animals.

Cannon and Manton (1927, 1929); Dennell (1933); Enquist (1949)

and Croker (1967a) all refer to "raptorial" feeding on occasion in essentially filter-feeding animals. The same occurs in *A. lawrenciana* since it has been known to feed off pieces > 4000 μ in size. The method employed in doing this, however, is unknown.

In filter-feeding a small current branches off from the main body current approaching the head of *A. lawrenciana* from the front and sides. This is created by the suction movement of maxilla 2 which also serves as the main filtering structure. Again, this is similar to *Haustorius* (Dennell 1933). Some of the suspended detritus caught up in the vortices recirculates towards the head and again moves posteriorly down the ventral surface. This may be of benefit to the animal in that the feeding apparatus gets more than one chance to filter food particles suspended in the water. It is particularly significant when organic material in the environment is scarce.

As Dennell (*op. cit.*) and Enquist (1949) describe for *Haustorius*, extensive burrowing beneath the substrate surface permits *A. lawrenciana* to utilize organic material in the substrate as well as in the water. Actual feeding was not observed in this position but it is likely that food particles adhere to mouthpart setae after being dislodged from the substrate into suspension in interstitial water by the action of the mouthparts, chiefly the gnathopods, as the animal burrows.

A. lawrenciana, on most occasions, after a short period of burrowing, came to rest with the head and associated structures above the surface at an angle of 35 degrees similar to the swimming orientation. Water currents continue to circulate as in swimming while the animal is in this position and it appears to filter-feed quite comfortably for

long periods. No other species described in the literature examined, except for the closely associated tube-feeding of *Haploops tubicola* Lilljeborg (Enquest 1949) and *Amplisca abdita* (Mills 1967), gets its food in this way.

At Salmon Cove *A. lawrenciana* were found to be primarily vegetarian. Carapaces of amphipods and detritus were found in the stomachs but the remainder was plant food. Since the species fed readily off animal as well as plant food at the laboratory, it is likely simply a case of utilization of the food types most easily obtained in its environment rather than a preference for plant food over animal food. Sameoto (1969a) found fine sand in the gut contents of *Neohaustorius biarticulatus* and *Haustorius canadensis* but no sand was found in any of the specimens of *A. lawrenciana* examined. Dennell (1933) simply says that *Haustorius* feeds on fine food particles and occasionally on large pieces but he makes no attempt to identify the food items. *Haustorius canadensis* and *Neohaustorius biarticulatus* feed primarily on detritus but diatoms, harpacticoid copepods, the remains of nematodes and sand grains were found in the stomach contents of specimens taken at Sippewissett Creek, Cape Cod (Sameoto 1969a). *Amplisca vadorum* and *Amplisca abdita* utilize diatoms, unicellular algae and partially degraded plant material as the main food sources at Barnstable Harbour, Massachusetts (Mills 1967).

A. lawrenciana prefers food of the particle-size range 125-250 μ since in experiments 85.7% of the animals offered food of this size range accepted it. Food larger than 500 μ was accepted by only a small percentage of animals. The fact that there was an

increase in the number of animals feeding on food particles > 4000 μ in diameter is one of the reasons why it has been concluded (page 112) that the species may feed on large pieces of food material at certain times.

Experiments have shown that the species is selective of food type as well of particle-size. It will take, for example, sea urchin (*Strongylocentrotus droebachiensis*) and the marine algae (*Laminaria*) over the blue mussle (*Mytilus*).

There appears to be only a slight correlation between the size of the animal and the distance between the setae of maxilla 2 and there is no relationship between size of the animal and size of food particles utilized. Distances between the seatae of maxilla 2 are much smaller than the size of food particles themselves.

Female *A. lawrenciana* slow the rate or cease feeding during reproductive periods particularly during the time of oogonia enlargement. This has important significance in that the energy normally expended in feeding is conserved during these periods and probably goes into ova production.

The experimental results in effect contradict the stomach analysis results in that they show that the species will select animal food as well as plant if it is available in the environment. *A. lawrenciana* can perhaps best be described as primarily an omnivorous filter-feeder.

The presence of molted integument in gut contents demonstrates that the animal may also at times be a scavenger-type feeder. In addition to providing a good food source at certain times of the year

this habit of ingesting molted integument, which is not uncommon in amphipods (D. H. Steele, pers. comm.), also provides an efficient recycling of energy from body wastes.

VI SUMMARY

Particle-size of the substrate and exposure of the beach are the chief limiting factors in the distribution of *Amphiporeia lawrenciana*, Shoemaker, 1929, in Newfoundland waters. Temperature, salinity and suspended matter in the seawater are not believed to be limiting factors. A narrow band of concentration of the species is present in the subtidal area at Salmon Cove beach 25 m. from HWS during the summer months. During the winter months the region of most dense concentration either shifts to deeper water or the animals burrow deeply into the substrate since few were taken in quantitative samples during this period. Temperature of the water and substrate is the variable most likely to cause this.

The population peak is reached in October when more than 90% of the population consists of young unsexable animals. The lowest numbers are present in the population in the nearshore area in January. Maximum life span is twelve months.

A. lawrenciana produces at least two broods per year. Oogonia of the first brood begins to enlarge inside the ovaries of females in October and November; the first embryos appear in brood pouches in March and the first young are released in August. Second brood embryos are deposited in brood pouches in June and young are released in September and October.

There is a correlation between the mean number of oogonia and embryos produced and length of females. Since the mean range of oogonia produced is 15.5 - 40.5 per female and the mean range of embryo

is 3.0 - 17.88 per female, a considerable number of the oogonia probably do not develop.

A. lawrenciana females can be easily distinguished during the reproductive phase apart from the fact that females are generally larger than males. The body assumes a number of color changes during this period. Males apparently are not affected and maintain the same body colors throughout their life span.

Copulation occurs as for *Gammarus dubeni* with the male attaching itself to the female at right angles.

There is a correlation of length with weight for both sexes. A considerably greater increase in weight with length exists, however, for ovigerous females than for males as shown by the slope of regression lines.

A. lawrenciana are more effective burrowers than swimmers. Observations have shown that water currents produced by the metachronial beat of three pairs of pleopods follow a distinct pattern and that a convenient means of aeration for young carried in the brood pouches of females is produced by the water currents which form two vortices in both sexes. The currents serve for both swimming and burrowing.

A. lawrenciana is primarily an omnivorous filter-feeder but it feeds chiefly on detritus; diatoms and algae particles at Salmon Cove. The species prefers food within a specific size range (125 - 250 μ) but there is only a slight correlation between the distance between the setae of maxilla 2, the chief filtering mouthpart, and length of the animal. There is also no evidence that larger animals ingest larger food particles. The species will on occasion feed

"raptorially" on large food particles and it ingests the molted integument either from its own body or from litter on the bottom.

Females apparently reduce the feeding rate or cease feeding completely while oogonia are developing and gradually resume feeding after the embryos have been deposited in the brood pouches. There is no evident degeneration of mouthparts during this period.

Preferred particle-size range of habitat substrate for *A. lawrenciana* is 125 - 2000 μ. More than 95% of the substrate at Salmon Cove is within the particle-size range of 125 - 1000 μ and the substrate found at areas of greatest abundance of the animal at beaches in Newfoundland is within the 125 - 1000 μ size range. Experiments show also that the species has an affinity for "home" substrate all other factors being constant.

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APPENDICES

Appendix 1a

Monthly seawater and substrate temperatures and salinities* at Salmon Cove

Date	Seawater Temperature, °C	Substrate Temperature, °C	Salinity, ppt.
Nov. 26, 1970	6.0	6.2	31.2
Dec. 31	1.0	1.5	26.1
Jan. 30, 1971	-1.0	-1.0	29.1
Feb. 27	-0.8	-0.8	17.8
Mar. 27	1.8	1.0	31.6
April 26	2.0	1.8	22.3
May 8	3.0	0.9	31.5
May 25	6.5	6.5	31.2
June 29	8.0	8.0	30.1
July 21	10.0	10.0	29.7
Aug. 17	10.0	10.0	30.1
Sept. 18	15.0	15.0	28.5
Oct. 23	6.8	6.8	29.4
Dec. 18	1.0	1.0	28.6
Mean	4.89	4.78	28.37

* mean of two samples

Appendix 1b

Monthly seawater suspended matter and substrate organic content at Salmon Cove

Date	Substrate Organic Content, %*	Seawater Suspended Matter, mg./l.
Nov. 26, 1970	3.44	--
Dec. 31	2.25	--
Jan. 30, 1971	2.87	8.4
Feb. 27	2.70	10.6
Mar. 27	2.29	7.1
April 26	4.19	5.4
May 8	2.00	12.1
May 25	2.25	11.3
June 29	1.99	22.0
July 21	4.11	12.5
Aug. 17	3.44	11.3
Sept. 18	2.64	21.0
Oct. 23	2.51	34.2
Dec. 18	2.47	21.3
Mean	2.80	14.76

* % of former dry weight

Appendix 1c

Dry weight (mg.) of substrate in eight grain-size classes (μ) for five substrate samples taken at Salmon Cove

Date	< 63	63-125	125-250	250-500	500-1000	1000-2000	2000-4000	> 4000
June 29	0.65	0.80	17.55	11.36	0.72	0.38	0.23	0.77
"	0.06	0.46	66.78	25.94	4.05	1.44	0.53	0.54
July 21	--	0.18	28.76	27.11	1.71	0.66	0.78	0.96
"	--	0.15	1.04	7.91	24.71	0.33	0.18	0.06
"	--	0.16	15.69	7.56	1.16	0.41	0.47	1.88
Mean Weight	0.12	0.35	25.97	15.98	6.47	0.65	0.44	0.85
%	0.24	0.70	51.10	31.44	12.73	1.27	0.86	1.66

Appendix 2

Depths burrowed by 33 *Amphiporeia lawrenciana*

Animal Length, mm.	Depth Burrowed, mm.	Animal Length, mm.	Depth Burrowed, mm.
10.0	7.5	8.0	2.5
7.5	5.0	7.5	5.0
9.0	7.0	7.5	4.0
9.5	6.0	8.5	6.0
9.5	10.0	9.0	6.5
9.0	5.0	7.5	6.0
10.0	15.0	7.5	3.5
9.5	3.5	8.0	5.0
8.0	5.0	7.5	7.5
9.0	6.0	8.5	8.0
10.0	6.5	7.5	5.0
8.5	7.5	9.0	13.5
7.5	4.5	9.5	14.0
9.0	12.0	6.5	4.5
10.0	10.0	6.5	3.5
8.0	4.5	7.5	4.5
7.0	3.5		
	Mean	8.12	6.59

Appendix 3

Stages and number of embryos and oogonia and females in the population

	1970 O	N	D	J	1971 F	M	A	M (1-8)	M (9-31)	J	J	A	S	O
Embryo Stage														
A	--	--	1	--	2	7	12	21	26	12	3	2	--	--
B	--	--	--	--	--	--	3	5	9	7	2	--	--	--
C	--	--	--	--	--	--	--	--	4	1	1	2	--	--
D	--	--	--	--	--	1	--	--	6	8	5	6	--	--
Hatched Young	--	--	--	--	--	--	--	--	3	6	8	7	--	--
Females														
Female- NS	33	40	42	9	25	12	23	12	5	--	--	12	34	42
Females-LS: with embryos	--	--	--	--	2	8	15	28	57	34	19	17	6	--
Females-LS: without embryos	--	--	--	--	--	2	1	--	9	6	22	12	--	--
Females-SS	--	--	--	--	1	--	1	--	--	--	--	--	--	--
Oogonia Class														
1	28	21	7	3	13	4	11	9	19	13	28	40	40	42
2	5	11	9	1	4	1	2	5	7	8	4	1	--	--
3	--	6	11	2	5	4	2	7	4	6	1	--	--	--
4	--	2	10	1	4	4	10	8	13	--	2	--	--	--
5	--	--	4	2	2	9	15	11	19	13	6	--	--	--

Appendix 4a

Total number of *Amphiporeia laurencina* collected per month in various length classes at Salmon Cove

Month	animal length (mm.)														Total/ 0.5m.^{2}
	1.5	2	3	4	5	6	7	8	9	10	11	12	13	14	
Oct., 1970	--	--	2	4	20	25	19	1	--	--	--	--	--	--	71
Nov. "	--	--	3	135	312	173	119	56	66	65	21	13	--	--	963
Dec. "	--	--	--	7	52	59	38	12	22	12	1	1	--	--	204
Jan., 1971	--	--	--	1	2	1	6	1	1	--	--	--	--	--	12
Feb. "	--	--	--	--	--	3	3	9	8	4	5	2	--	--	34
Mar. "	--	--	--	--	4	16	5	22	12	4	3	1	--	--	67
April "	--	--	--	1	29	55	37	57	34	18	4	3	--	--	238
May (1-15) "*	--	--	--	--	23	91	56	68	65	35	16	7	4	--	365
May(16-31) "	--	--	--	--	21	55	83	49	58	32	16	15	5	1	335
June "	40	368	88	3	12	80	33	61	61	33	10	2	1	--	792
July "	4	368	234	21	4	23	31	72	85	50	28	7	1	--	928
Aug. "	13	55	184	92	20	28	21	34	40	20	10	3	--	--	520
Sept. "	23	118	502	281	178	31	19	27	34	21	9	--	--	--	1243
Oct. "	--	--	34	758	750	164	95	18	46	44	9	4	--	--	1922
	80	909	1047	1303	1427	804	566	486	532	338	132	58	11	1	7694

* Not shown in the graphs

Appendix 4b

A. lawrenciana: total number of males collected per month in various length classes at Salmon Cove (Number per 0.5m.^{2})

Month	Length (mm.)							Total Number of Animals/0.5m.^{2}/month
	4.0	5.0	6.0	2.0	8.0	9.0	10.0	
Oct. 1970	1	9	7	4	1	--	--	22
Nov. "	1	14	12	7	4	1	--	39
Dec. "	7	37	35	10	2	--	--	91
Jan. 1971	1	1	--	--	--	--	--	2
Feb. "	--	--	3	3	--	2	--	8
Mar. "	--	4	14	1	1	--	1	21
Apr. "	1	29	54	15	4	--	--	103
May (1-15)* "	--	23	89	35	2	1	--	150
May(16-31) "	--	21	53	67	6	--	--	147
June "	--	11	72	23	1	--	--	107
July "	--	3	23	23	6	--	--	55
Aug. "	--	--	13	15	2	--	--	30
Sept. "	--	1	12	18	--	--	--	31
Oct. "	--	6	8	27	4	--	--	45
	11	159	395	248	33	4	1	851

* Not shown in the graphs

Appendix 4c

A. lawrenciana: total number of females without long sctae on oostegites collected per month at Salmon Cove (Number per 0.5m.^{2})

Month	Length (mm.)									Total number of Animals/0.5m.^{2}/month
	4.0	5.0	6.0	7.0	8.0	9.0	10.0	11.0	12.0	
Oct., 1970	4	14	15	--	--	--	--	--	--	33
Nov. "	1	19	67	102	51	65	65	21	13	404
Dec. "	--	14	24	28	10	21	11	1	1	110
Jan., 1971	--	1	1	5	1	1	--	--	--	9
Feb. "	--	--	--	--	9	5	3	4	2	23
Mar. "	--	--	2	4	17	5	3	--	--	31
Apr. "	--	--	1	21	45	22	3	--	--	92
May* (1-15) "	--	--	2	13	23	10	1	--	--	49
May (16-31) "	--	--	2	7	3	--	--	--	--	12
June "	--	--	--	2	--	--	--	--	--	2
July "	--	--	--	1	--	--	--	--	--	1
Aug. "	--	--	2	3	10	22	6	1	1	45
Sept. "	--	--	--	1	25	31	21	5	--	83
Oct. "	--	1	5	8	14	46	44	9	4	131
	5	49	121	195	208	228	157	41	21	1025

* Not shown in Fig.

Appendix 4d

A. lawrenciana: total number of females with long setae and embryos in brood pouches collected per month at Salmon Cove (Number per 0.5m.^{2})

Month	Length (mm.)								Total number of Animals/0.5m.^{2}/month
	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0	
Oct. 1970	--	--	--	--	--	--	--	--	--
Nov. "	--	--	--	--	--	--	--	--	--
Dec. "	--	--	1	1	--	--	--	--	2
Jan. 1971	--	--	--	--	--	--	--	--	--
Feb. "	--	--	--	--	1	--	--	--	1
Mar. "	--	1	2	2	3	1	--	--	9
Apr. "	--	6	9	15	4	3	--	--	37
May* (1-15) "	8	41	52	34	16	7	4	--	162
May (16-31) "	9	40	56	32	15	15	5	1	173
June "	6	53	50	29	9	1	1	--	149
July "	1	29	47	28	16	1	1	--	123
Aug. "	--	9	12	8	2	1	--	--	32
Sept. "	--	--	--	--	--	--	--	--	--
Oct. "	--	--	--	--	--	--	--	--	--
	24	179	229	149	66	29	11	1	688

* Not shown in Fig.

Appendix 4e

A. lawrenciana: total number of females with long setae and without embryos collected per month at Salmon Cove (Number per 0.5m.^{2})

Month	Length (mm.)								Total Number of Animals/0.5m.^{2}/month
	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0	
Oct. 1970	--	--	--	--	--	--	--	--	--
Nov. "	--	--	--	--	--	--	--	--	--
Dec. "	--	--	--	--	--	--	--	--	--
Jan. 1971	--	--	--	--	--	--	--	--	--
Feb. "	--	--	(1)*	(1)	--	--	--	--	2
Mar. "	--	2(1)	4(1)	1	--	--	--	--	9
Apr. "	1	2	2(1)	--	--	--	--	--	6
May** " (1-15)	--	(2)	(2)	--	--	--	--	--	4
May " (16-31)	--	--	2	--	1	--	--	--	3
June "	2	7	11	4	1	1	--	--	26
July "	6	37	38	22	12	6	--	--	121
Aug. "	--	13	6	6	7	1	--	--	33
Sept. "	--	2	3	--	4	--	--	--	9
Oct. "	--	--	--	--	--	--	--	--	--
	9	66	71	34	25	8	--	--	213

* Numbers in brackets show females with short setae

** Not shown in Fig.

Appendix 4f

A. lawrenciana: total number of unsexables collected per month at Salmon Cove

Month	Length (mm.)								Total Number of Animals/0.5m.^{2}/month
	1.5	2.0	3.0	4.0	5.0	6.0	7.0	8.0	
Oct. 1970	--	--	2	3	7	4	--	--	16
Nov. "	--	--	3	133	279	94	10	1	520
Dec. "	--	--	--	--	1	--	--	--	1
Jan. 1971	--	--	--	--	--	--	1	--	1
Feb. "	--	--	--	--	--	--	--	--	--
Mar. "	--	--	--	--	--	--	--	--	--
Apr. "	--	--	--	--	--	--	--	--	--
May* " (1-15)	--	--	--	--	--	--	--	--	--
May " (16-31)	--	--	--	--	--	--	--	--	--
June "	40	368	88	3	1	8	--	--	508
July "	4	368	234	21	1		--	--	628
Aug. "	13	55	184	92	20	13	3	--	380
Sept. "	23	118	502	281	177	19	--	--	1120
Oct. "	--	--	34	758	743	151	60	--	1746
	80	909	1047	1291	1229	289	74	1	4920

* Not shown in Fig.

Appendix 5a

Summary of physical factors at 29 beach areas in insular Newfoundland

Beach Number	Temperature		Salinity o/oo	Water Suspended Matter mg./l.
	Water, °C	Substrate, °C		
1	12.7	12.0	27.1	40.2
2	13.0	12.2	26.5	--
3	13.7	12.0	26.9	25.8
4	14.2	12.2	26.5	18.0
5	14.0	12.0	26.3	--
6	19.0	16.0	26.2	27.6
7	9.7	10.2	30.2	11.2
8	12.0	11.8	27.7	--
9	12.3	11.8	28.3	39.6
10	11.2	12.0	28.2	36.0
11	11.0	11.0	28.6	8.4
12	12.7	12.2	25.6	22.0
13	15.7	15.0	5.0	12.6
14	12.0	12.2	26.3	8.4
15	14.8	14.0	26.2	22.0
16	16.0	13.0	13.7	14.6
17	10.5	10.7	27.8	27.0
18	14.0	14.3	21.8	9.0
19A	13.0	12.8	26.2	64.4
19B	16.5	14.8	21.7	--

Appendix 5a (Continued)

Beach Number	Temperature		Salinity o/oo	Water Suspended Matter mg./l.
	Water, °C	Substrate, °C		
20A	16.2	15.8	10.0	77.8
20B	7.8	8.8	30.2	64.4
21	24.0	21.0	29.0	11.2
22	15.0	14.0	23.4	9.7
23	17.5	17.3	28.6	58.2
24	15.8	15.8	27.7	9.2
25	17.0	16.0	27.8	8.1
26	13.0	12.8	30.2	2.0
27	13.2	13.8	29.5	11.8
28	18.0	17.0	6.2	8.6
29	17.5	17.5	28.6	24.1

Appendix 5b

Summary of per cent particle-size of substrate data at 29 beach areas in insular Newfoundland. Weights are given in milligrams.

Beach Number	Particle Size, μ							
	≤ 63	63-125	125-250	250-500	500-1000	1000-2000	2000-4000	> 4000
1	--	0.21	45.24	52.64	1.35	0.40	0.16	--
2	--	0.04	0.05	2.65	32.65	31.00	21.39	12.22
3	--	0.56	71.45	18.06	5.15	3.34	1.44	--
4	1.00	12.75	75.39	6.87	1.69	1.33	0.97	--
5	--	0.51	17.53	7.40	30.06	36.84	7.66	--
6	--	--	0.07	0.06	15.27	53.99	26.24	4.35
7	0.06	0.08	0.13	7.06	52.43	31.50	8.32	0.42
8	0.35	1.44	26.39	10.72	13.98	22.84	14.13	10.15
9	0.47	2.94	16.94	26.78	20.91	14.27	9.89	7.90
10	0.01	0.18	7.97	13.51	37.43	20.23	10.38	10.29
11	0.07	1.71	32.80	10.00	13.87	20.88	12.20	8.47
12	0.09	0.30	7.59	34.96	13.24	17.67	13.49	12.76
13	0.40	1.01	16.66	44.03	23.76	8.43	4.43	1.28
14	0.36	7.33	57.31	9.36	0.67	0.98	7.51	16.48
15	--	--	0.02	0.11	2.20	12.76	22.96	61.95
16	0.55	2.03	21.01	32.35	11.49	9.50	4.52	18.55
17	--	0.12	1.94	22.74	37.00	24.46	9.69	4.05
18	--	0.06	10.18	15.09	11.32	12.74	9.67	40.94
19B	0.06	0.10	2.60	32.10	31.54	24.60	7.30	1.70

Appendix 5b (Continued)

Beach Number	Particle Size, μ							
	< 63	63-125	125-250	250-500	500-1000	1000-2000	2000-4000	> 4000
20A	0.78	2.28	37.87	48.30	5.93	3.49	1.29	0.06
20B	--	--	0.02	9.52	65.64	24.68	0.14	--
21	0.05	0.55	49.36	48.04	0.30	0.18	0.43	1.09
22	--	0.01	21.58	59.45	16.42	1.55	0.79	0.20
23	--	--	--	0.15	25.26	35.90	37.63	1.06
24	--	--	--	22.42	32.92	24.15	20.51	--
25	--	12.44	20.47	14.43	13.43	13.14	13.34	12.75
26	--	--	15.64	17.56	17.44	16.90	15.93	16.53
27	--	--	--	--	--	--	--	--
28	--	12.44	12.90	20.06	15.97	13.69	12.49	12.45
29	--	--	18.19	20.29	16.64	15.49	15.11	14.28

Appendix 6a

A. lawrenciana: average weight per body length for females

Length, mm.	1	2	3	Average Weight, mg./f.
5	2.5	2.0	2.0	2.20
6	3.0	3.2	2.0	2.70
7	4.8	3.0	3.8	3.90
8	7.8	9.8	7.4	8.30
9	7.5	9.8	12.0	9.80
10	10.6	10.5	9.2	10.10
11	23.2	20.3	12.4	18.60
12	25.0	27.7	23.1	25.30
13	24.5	30.0	25.0	26.50
14	--	37.8	37.0	37.40

Appendix 6b

A. lawrenciana: average weight per body length for males

Length, mm.	1	2	3	Average Weight, mg./m.
5	0.8	0.4	1.0	0.73
6	1.1	1.5	1.6	1.40
7	1.9	--	--	1.90
8	6.6	4.0	3.5	4.70
9	6.8	8.3	6.5	7.20

Appendix 7

Food types found in the stomachs of 38 *Amphiporeia lawrenciana* and per cent of animals with each

length (mm.)	detritus	exuvia	diatoms	algae		
				unicell.	filamen.	multicell
10.0	✓	✓	.	.	.	.
7.5	✓	✓	✓	.	.	.
9.0	.	✓	.	.	.	.
9.0	✓	.	.	.	✓	.
9.5	✓	.	.	.	✓	.
8.5	.	✓	.	.	✓	.
7.5	✓	.	✓	.	✓	.
8.0	.	.	✓	.	✓	.
10.0	✓	.	.	.	.	.
11.0	.	.	✓	.	✓	✓
9.0	✓	.	.	.	.	.
8.5	✓	.	.	.	.	.
9.5	✓	.	.	.	.	.
10.0	✓	.	.	.	.	.
9.0	.	✓	✓	.	✓	.
9.0	.	✓	.	.	.	.
7.5	✓	✓	✓	.	.	.
8.0	.	✓	.	.	.	.
8.0	.	.	.	.	.	.
8.5	✓	✓	.	.	.	.

Appendix 7 (Continued)

length (mm.)	detritus	exuvia	diatoms	algae		
				unicell.	filamen.	multicell
8.5	.	✓	.	.	✓	.
7.0	.	✓	.	.	✓	.
8.0	.	.	.	✓	.	.
8.5	✓	✓	.	✓	✓	.
9.0	✓	✓	.	✓	✓	✓
12.5	.	✓	.	.	.	✓
9.0	✓	✓	.	.	.	.
13.0	✓	✓	.	✓	.	.
13.0	✓	.	✓	.	.	.
9.0	✓	✓	.	.	.	.
5.0	✓	✓	✓	.	.	.
10.0	✓	✓	.	✓	.	.
6.5	✓	.	.	.	.	.
7.0	✓	.	.	.	.	.
7.5	.	✓	✓	.	✓	.
7.5	✓	.	.	.	.	.
8.0	.	✓	.	✓	✓	.
4.0	✓	✓	.	.	.	.
	% 63.16	57.90	23.68	15.79	34.21	7.90

Appendix 8a

Number of *Amphiporeia lawrenciana* ingesting food of eight particle-size ranges in three experiments

	Particle size (μ)							
	< 63	63-125	125-250	250-500	500-1000	1000-2000	2000-4000	> 4000
Experiment 1:								
Number of Animals/Container		3	3	3	2	3	3	3
Number of Animals Ingesting/Container		3	3	3	1	2	2	2
Experiment 2:								
Number of Animals/Container	6	5	6	6	6	6	6	
Number of Animals Ingesting/Container	5	3	4	3	2	0	0	
Experiment 3:								
Number of Animals/Container	4	5	5	5	5	5	5	4
Number of Animals Ingesting/Container	0	3	5	1	2	0	0	0
Total Number Animals/Container	10	13	14	14	13	14	14	7
Total Number Ingesting/Container	5	9	12	7	5	2	2	2
% Ingesting	50.0	69.2	85.7	50.0	30.8	14.3	14.3	28.6

Appendix 8b

Number of animals of three size ranges ingesting food material of one size range (63-125 μ)

	Animal size, mm.		
	5.65 (small)	7-8.5 (medium)	9-10.5 (large)
Experiment 4:			
No. of animals/container	10	10	10
No. animals ingesting	1	8	6
Experiment 5:			
No. of animals/container	10	10	10
No. animals ingesting	8	7	4
Total no. animals/container	20	20	20
Total no. ingesting	9	15	10
% ingesting	45.0	75.0	50.0

Appendix 8c

Number of females with and without embryos of three size ranges ingesting food material of one size range (63-125 μ)

	Animal size, mm.		
	5-6.5 (small)	7-8.5 (medium)	9-10-5 (large)
No. females/container	10	10	10
No. of females with embryos ingesting	0	4	4
% ingesting	0	40	40
No. of females without embryos ingesting	10	0	0
% ingesting	100	0	0

Appendix 8d

Number of *A. lawrenciana*, males and females of four types, ingesting food of particle-size 250-500 μ

Number of Animals/Container	Sex	Type	Length, mm.	Number of Animals Ingesting/Container	%
5	Male		5.0-6.5 (Mean-5.8)	2	40
5	Female	With long setae Without Embryos	7.0-8.5 (Mean-7.2)	3	60
5	Female	With A-Stage Embryos	7.0-7.5 (Mean-7.3)	1	20
5	Female	With D-Stage Embryos	7.5-9.0 (Mean-8.1)	4	80
5	Female	With Hatched Young	7.5-9.0 (Mean-8.5)	5	100

Appendix 9a

Mean distance (μ) between the setae of the inner and external lobes of maxilla 2 of one 9 mm. female *Amphiporeia lawrenciana*

Inner Lobe		External Lobe Setae
Medial Setae	Marginal Setae	
9	6	18
	9	6
12	9	9
	9	6
12	6	6
	9	9
12	15	3
	12	3
12	9	6
	9	6
6	6	6
	6	6
12	6	3
	6	3
15	9	3
	6	3
9	6	3
		6
		3
		3
Mean 11.00	8.12	5.55
S.E. .00	.04	.00

Appendix 9b

Mean distance (μ) between the setae of the inner and external lobes of maxilla 2 of 17 specimens of *Amphiporeia lawrenciana*

Animal Length, mm.	Inner Lobe		External Lobe Setae
	Medial Setae	Marginal Setae	
7.5	11.00	8.12	5.55
8.0	10.80	8.37	7.05
9.0	8.18	7.66	7.06
8.0	11.10	9.00	5.50
11.0	10.90	7.93	6.71
12.0	8.20	9.60	6.35
6.0	5.68	7.50	4.88
9.0	9.60	7.43	6.79
12.0	7.50	8.31	7.65
7.5	10.20	7.67	4.94
8.0	9.00	7.32	5.63
7.0	8.18	7.00	7.11
11.0	8.31	8.80	7.50
10.0	8.75	7.15	8.71
7.0	8.10	7.93	6.57
6.5	9.33	6.00	6.69
10.0	8.54	7.94	5.43
Mean		Mean (weighted)	
8.25	8.90	7.91	6.49

Appendix 10

Number of *Amphiporeia lawrenciana* ingesting six different food types
(Particle-size range: 125 - > 4000 μ)

Food Type Offered	Number of Animals/Container			Total	Number of Animals Ingesting/Container			Total	% Ingesting
	Small (5-6.5 mm.)	Medium (7-8.5 mm.)	Large (9-11 mm.)		Small	Medium	Large		
Macoma (with shell)	3	3	3	9	1	1	1	3	33.3
Placopecten (without shell)	"	"	"	"	1	0	1	2	22.2
Mytilus (without shell)	"	"	"	"	0	0	0	0	0
Strongylocentrotus (with test)	"	"	"	"	0	0	3	3	33.3
Strongylocentrotus (without test)	"	"	"	"	1	3	3	7	77.8
Laminaria	"	"	"		2	0	2	4	44.4
Total	18	18	18	45	5	4	10	19	42.2

Appendix 11a

Results of six experiments on substrate color selection in *Amphiporeia lawrenciana*

Experiment Number	Date	Number of Animals Used	Number in Red Substrate	Number in Black Substrate	Number in Green Substrate	Number found outside Substrate Containers
1	May 11, 1971	60	16	18	16	10
2	" 12 "	60	42	8	7	3
3	" 13 "	60	10	21	20	9
4	" 14 "	90	27	43	18	2
5	" 17 "	90	29	31	22	7
6	" 18 "	90	22	37	28	3

Appendix 11b

Results of five separate control experiments run in conjunction with the six substrate color selection experiments using incinerated material (600° C.) unsorted and the same color

Experiment Number	Number of Animals Used	Container Number							Number found outside Substrate Container
		1	2	3	4	5	6	7	
1	140	6	2	4	9	26	18	13	62
2	140	10	9	6	7	4	9	23	52
3	140	5	3	3	10	11	11	10	87
4	140	17	16	16	9	8	4	12	58
5	140	24	16	15	27	15	29	14	--
	700	62	46	44	62	64	71	72	279

Appendix 12a

Results of five separate substrate selection experiments using incinerated material (24 hours at 600° C.) of seven different size ranges

Experiment Number	Number of Animals Used	Container Number							Number found outside Substrate Container
		1	2	3	4	5	6	7	
1	140	32	20	7	8	3	15	5	50
2	140	4	28	16	14	12	2	2	62
3	140	2	16	18	14	32	1	0	57
4	140	3	10	20	26	35	5	3	38
5	140	14	26	18	18	16	13	14	21
Total	700	55	100	79	80	98	36	24	228

Appendix 12b

Results of seven separate substrate selection experiments using dried material (24 hours at 60° C.) of seven size ranges; six mixtures and unsorted material from Salmon Cove

Experiment Number	Number of Animals Used	Container Number														Number found outside Substrate Container
		1*	2	3	4	5	6	7	A+	B	C	D	E	F	X°	
1	280	1	6	9	79	31	3	1	5	2	4	13	1	1	87	37
2	"	6	40	42	28	13	3	1	28	22	26	26	4	1	35	15
3	"	3	34	31	34	6	12	0	27	53	29	20	7	1	32	4
4	"	5	30	46	27	9	0	0	42	21	26	13	3	0	51	7
5	"	10	26	49	20	13	2	5	22	27	17	22	8	1	15	43
6	"	9	14	22	41	33	4	6	34	22	26	19	4	5	24	17
7	"	9	25	19	45	13	11	3	50	25	28	18	7	5	20	3
	1960	43	175	218	274	118	35	16	208	172	156	129	34	14	264	126

* 1-7 contained material of a specific size range (See Table 4).

\+ A-F contained mixtures (See Table 4).

° unsorted material from Salmon Cove.

Appendix 12c

Results of five separate control experiements run in conjunction with the seven substrate selection experiments of the second series

Experiment Number	Number of Animals Used	Container Number							Number found outside Substrate Container
		1	2	3	4	5	6	7	
1	140	12	17	9	16	5	41	5	35
2	"	11	14	11	34	11	21	17	21
3	"	10	19	12	24	16	35	14	10
4	"	14	12	10	26	11	28	36	3
5	"	10	20	14	25	13	24	19	15
	700	57	82	56	125	56	149	91	184